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#### Errata

p. 248, last line: for *Cuburbita* read *Cucurbita*.

p. 249, l. 15 from bottom: for *Eschscholtzia* read *Escholtzia*.

p. 357, l. 27: for *sacoptoides* read *sarcoptoides*.

p. 368, l. 4 from bottom: for 10 read 16.

TRIPLOID MUTANTS AMONG DIPLOID SEEDLING  
POPULATIONS OF *ASIMINA TRILOBA*<sup>1</sup>WRAY M. BOWDEN<sup>2</sup>

The North American papaw, *Asimina triloba* (L.) Dunal, is an especially interesting species because it is the only member of the family Annonaceae that is hardy in New York, Michigan, and southern Ontario. The Annonaceae are mainly a tropical and subtropical family with a small number of species in the southeastern United States. Locke (10) observed  $n = 9$  and Bowden (3, 4) determined  $n = 9$ ,  $2n = 18$  in *Asimina triloba*. Locke's counts were made from material collected near Mississippi State College and near Smith, Indiana; those of Bowden were made from the collection of papaw trees, from various sources, at The Blandy Experimental Farm, Boyce, Virginia. It seemed desirable to ascertain if there was any variation in chromosome number in populations of the species throughout its natural range. Requests for fruits and seeds were made in September, 1945 and 1946; twenty-three collections were received.

**Material.** The natural range of *Asimina triloba* is from New York State south to northern Florida, and from Nebraska to south-eastern Texas. The tree is rare in south-eastern Texas and northern Florida. Figure 1 shows the distribution of the collections examined as well as those studied by Locke (10). All material originated from wild plants except those from the trees cultivated at Geneva, New York. The southernmost part of the species range is not well represented. The collections from Michigan, southern Ontario, and New York, were from wild populations near or at the northern limits of the species range.<sup>3</sup>

<sup>1</sup> Contribution No. 939 from the Division of Botany and Plant Pathology, Science Service, Department of Agriculture, Ottawa.

<sup>2</sup> Assistant Botanist (Cyto-genetics).

<sup>3</sup> The collectors and localities from which the material was obtained are as follows; the numbers of seedlings examined cytologically are shown in parentheses. D: G. H. Hamilton; woods below Queenston Heights Park, Queenston, Lincoln County, Ontario (10). E: Dr. W. C. Coker; Chapel Hill, Orange County, North Carolina; (6). F: L. J. Gier; South of city limits of Liberty, Clay County, Missouri (6). G: Dr. F. A. Clarkson; through L. Van Kleemput; collected at Eighth Concession, Niagara Township, Lincoln County, Ontario; (3). H: R. A. Breuer; bluffs of Missouri River, Herman, Gasconade County, Missouri (6). I: Dr. G. L. Slate; Cultivated in papaw orchard, seed from best varieties, New York Agricultural Experiment Station, Geneva, New York; pkt. No. 1 (7). J: Same source as I: pkt. No. 2 (5). K: Mrs. E. J. Musseden; tree in orchard, Illiopolis, Sangamon County, Illinois (5). L: Miss P. E. Van Winkle; Shelbyville, Shelby County, Indiana (6). M: Miss A. Huber; Dubois Farm, near Wabash, Wabash County, Indiana (3). N: I. R. Hunter; five miles east of Dowagiac, Cass County, Michigan (7). O: Mrs. D. T. Ransdell; Lawrence, Douglas County, Kansas

**Methods.** The seeds were separated from the pulp, placed in a sand-peat mixture in labelled pots, and transferred to gold storage for stratification for a period of about five months. Temperature was kept above the freezing point but low enough to obtain satisfactory stratification. The

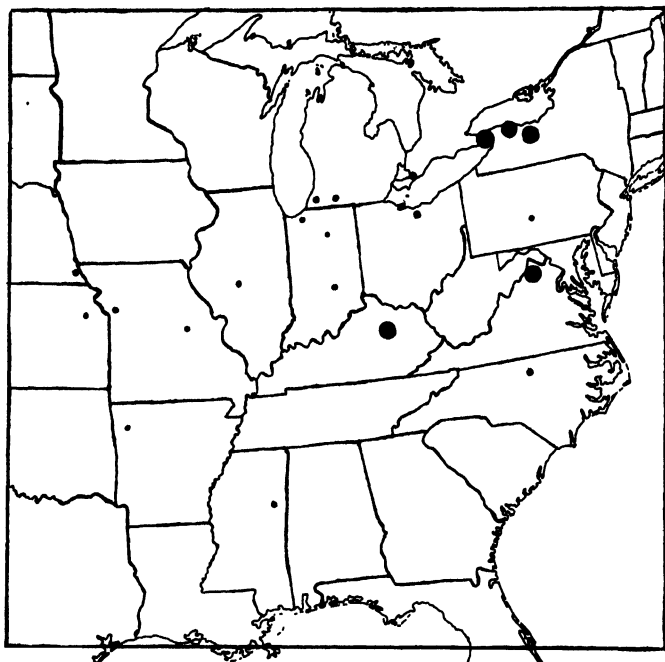


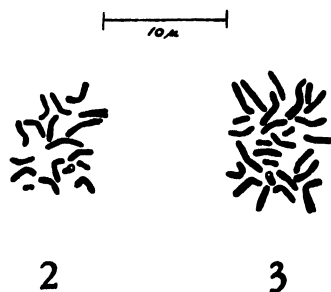
FIG. 1. Distribution of collections of *Asimina triloba*. Symbols: large dots—diploid populations with single triploid mutants; small dots—diploid populations. The collections reported in this paper are shown and the two collections of Locke (10).

seeds were removed from the cold cellar in March, reotted in a peat-soil mixture suitable for seedlings, and placed in the greenhouse. Several temperatures were tried; much better seedling growth was obtained in a warm house than in a cool one. The seeds germinated well in almost all of the

(4). P: Mrs. A. E. Shenk; farm of Jesse Ash, Quincy, Branch County, Michigan (4). Q: W. F. Brinker; near Spencer, Black River Valley, Medina County, Ohio (3). R: W. A. Smith; near Brockport, Monroe County, New York (4). S: D. M. Moore; near St. Paul, Madison County, Arkansas (3). T: Dr. F. T. McFarland; three miles west of Clay City, Powell County, Kentucky (9). U: A. A. Wood; from trees two miles south-east of Chatham, Kent County, Ontario (43 seedlings from 12 fruits). V: Mrs. E. G. Noble; Brownsville, Nemaha County, Nebraska (9). W: Dr. G. L. Slate; cultivated in papaw orchard; New York Agr. Exp. Stat., Geneva, New York (46 seedlings from 10 fruits from 10 trees). X: G. H. Hamilton, through Dr. W. S. Fox; near Queenston, Lincoln County, Ontario (4). Y: H. W. Copenhaver; above Front Royal, banks of Shenandoah River, Warren County, Virginia (10). Z: Dr. F. D. Kern; Colerain State Park, Spruce Creek, Huntingdon County, Pennsylvania (2).

collections. This satisfactory result was due to the freshness of the seeds and an adequate stratification period.

The seedlings were grown until an optimum level of mitotic activity was reached. Some of the seeds were slower in germinating or in producing active root-tips so that it was not possible to fix root-tips of all seedlings in each collection. Root-tips from all vigorous seedlings in each population were fixed in Belling's modification of Nawashin's fixative, embedded according to La Cour's alcohol-chloroform-paraffin schedule, sectioned at a thickness of  $10\ \mu$ , and stained by La Cour's iodine-crystal violet schedule. In fixing the root-tips, improved fixation was obtained in some roots by cutting them longitudinally, and in others by removing the root-cap region before fixing. Most of the root-tips showed large numbers of metaphases in the most active mitotic region. The root-tips of each collection were embedded in groups with three or four root-tips in each series. This procedure was a great aid in reducing the amount of handling and the quan-



FIGS. 2 and 3. Camera lucida drawings of mitotic metaphases in periblem cells of root tips. FIG. 2. Diploid ( $2n=18$ ) from seedling No. 2, population X, Queenston, Ontario. FIG. 3. Triploid ( $2n=27$ ) from seedling No. 1, population X, Queenston, Ontario.

tity of materials required. Smear methods were tried on papaw root-tips, but were not satisfactory, although the same methods gave good results with *Crepis capillaris*, *Vicia Faba*, and *Trillium grandiflorum*. All examinations were carried out with an oil-immersion lens. The use of Wratten filter No. 60 (green) in combination with Wratten filter E No. 22 (deep orange) facilitated the observations. The drawings were made by use of a Spencer research microscope equipped with a  $90\times$  oil-immersion objective, N.A. 1.30, and  $12\times$  ocular.

**Results.** Somatic chromosome numbers were determined in root tips of 205 seedlings from 23 collections. Large numbers of metaphases were examined in all tissues of each root tip. In 18 collections, 171 seedlings were diploid ( $2n=18$ ). In collections I, R, T, X and Y, 29 seedlings were diploid, and 1 seedling in each was triploid ( $2n=27$ ). Thus, of 205 seed-



lings examined, 200 were diploids and 5 were triploids. The frequency of triploidy was 2.4 per cent or 1 triploid per 40 diploids.

The camera lucida drawings in figures 2 and 3 were made from plates that were chosen because chromosome morphology could be observed well in them. In many plates, a few of the chromosomes tended to lie close together and made interpretation difficult. There was also a tendency for the smaller chromosomes to lie obliquely or vertically so that a careful analysis of many plates was carried out before the drawings were completed. In a few plates, the nucleolus persisted to mid-metaphase. One or two small chromosomes were sometimes associated with the nucleolus and were seen to lie alongside it, often obliquely or vertically.

A comparison of figures 2 and 3 shows that the area of a triploid plate is larger than that of a diploid plate. All five triploid roots showed this greater plate area. Four of the triploid roots were comparable in size to the diploid roots. The triploid root from population X was larger than any of the three diploid roots from the same collection. In the diploid complement of *Asimina triloba*, there are two large chromosomes and two very small ones. In the triploid metaphase, three large and three very small chromosomes were observed. The range of chromosome size and morphology is shown in figures 2 and 3.

**Discussion.** Löve (11) stated that "within almost all plant species, individuals with an autotriploid number of chromosomes may be met with in nature in a very low frequency." Nawashin (15) examined 2,000 plants of *Crepis capillaris*; 1,989 were diploid ( $2n = 6$ ) and 11 (0.55%) were triploid ( $2n = 9$ ). Giles (5) studied 59 collections of *Cuthbertia graminea* and found 27 diploid plants, 1 triploid, 129 tetraploids, two hexaploids, and two aneuploids, that is, one triploid (0.62%) among 161 plants. Baldwin (1) examined 71 collections of *Sedum ternatum* and reported that 11 collections were diploid, 57 tetraploid, two triploid, and one was hexaploid; or 2.8% were triploids. Baldwin and Culp (2) found that seedlings grown from 7 collections of seeds from single-tree collections of *Diospyros virginiana* were tetraploid ( $2n = 60$ ) and seedlings from 17 collections were hexaploid ( $2n = 90$ ). Johnsson (7) selected twin, triplet, and quadruplet seedlings from more than 75,000 acorns of *Quercus robur*. Of these, 728 seedlings were diploid ( $2n = 24$ ) and three (0.41%) were triploid ( $2n = 36$ ). Müntzing (14) found that triploids were the commonest mutants in those twin seedlings which showed a deviating chromosome number. He observed that, in different species, there was a different frequency of chromosome number aberrants. Triploids occurred with high frequency in *Asimina triloba*: 200 diploids and 5 triploids, or 2.4 per cent triploids. The triploid mutants were not, however, distributed evenly in the populations; single

triploids were found in two populations with only four seedlings in each, while populations with 43 and 46 seedlings were all diploid. It is not known at present if any wild trees of *Asimina triloba* exist as triploid or possibly tetraploid individuals.

Triploids may arise in several different ways. De Mol (12) obtained unreduced pollen grains by digging unripe hyacinth bulbs and giving them a warm temperature treatment. The abnormal pollen was used to pollinate a diploid and 76 diploids and 3 triploids were obtained from the seed. Krug (9) summarized the work done on the subfamily Aurantioideae and found that more than 50 triploids have been observed in the genus *Citrus*. Some of these were produced by crossing diploids with tetraploids. About forty of the triploids were hybrids between diploid varieties and were thought "to have originated by non-reduction perhaps in megasporocytes." Müntzing (13) stated that "if an unreduced embryo sac is fertilized at the same time as the reduced one, the typical result will be obtained: one diploid and one triploid seedling." Two embryo-sacs may be present in the nucellus instead of one. He stated further that "if the twin plants differ in chromosome number, one of the twins is generally triploid in relation to the other one. This may be due to simultaneous fertilization of reduced and unreduced embryo sacs." Kostoff (8) suggested that triploids may develop from the endosperm. Ishikawa (6) observed the fusion of an egg nucleus with two male nuclei in *Oenothera*.

The triploid papaws occurred in areas where the temperature may have fluctuated considerably during the early spring season when meiosis was taking place in *Asimina triloba*. It is possible therefore that gametes from either unreduced pollen grains or unreduced embryo-sacs may have fused with normal reduced gametes to produce the triploids. If tetraploids occurred in the wild, it is obvious that they could have produced gametes with the two sets of chromosomes which, upon fusing with haploid gametes, would have formed triploid zygotes.

The author expresses his appreciation for the suggestions of Dr. Orland E. White, Director, The Blandy Experimental Farm, The University of Virginia, Boyce, Virginia; the aid of The Journal of Heredity and The Home Garden Magazine in collecting seeds; and the co-operation of collectors.

#### SUMMARY

Somatic chromosome numbers were determined in root tips of 205 seedlings of the North American papaw, *Asimina triloba* (L.) Dunal, that were grown from 23 collections of seeds. In eighteen collections, 171 seedlings were diploid ( $2n = 18$ ). In five collections, 29 seedlings were diploid,

and 1 seedling in each was triploid ( $2n = 27$ ). There was an average of one triploid per forty diploids.

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## THE SOMATIC CHROMOSOMES OF SARRACENIA

ADOLPH HECHT

The carnivorous aspects of the *Sarracenias* have been studied extensively, but the writer knows of only two papers in which any attention has been paid to the cytology of these plants. Shreve (1906) counted 12 chromosomes in the pollen mother cells of *Sarracenia purpurea*,<sup>1</sup> and Nichols (1908) reported this same count ( $n = 12$ ) for *S. rubra* and *S. variolaris*.<sup>2</sup> Russell (1919) studied the anatomical characteristics of several species-hybrids of the genus, but made no chromosome counts. Lloyd (1942) reviewed the literature dealing with the general vegetative anatomy of the *Sarracenias*, but made no mention of cytological details. In Uphof's (1936) discussion of the genus in *Die natürlichen Pflanzenfamilien* the chromosome counts mentioned above are listed, but no additional studies are cited. Darlington and Janaki-Ammal (1945) list two species of *Sarracenia*, *S. drummondii* and *S. flava*, but with a blank in their column for chromosome number.

Six species of *Sarracenia* were identified in the flora of western Florida with the aid of Small's (1933) manual. These are *S. purpurea* L.,<sup>3</sup> *S. psittacina* Michx., *S. drummondii* Croom, *S. flava* L., *S. jonesii* Wherry, and *S. rubra* Walt. The present study involves these six species together with a form intermediate between *S. drummondii* and *S. flava*. The first five of these species and the intermediate form were commonly found growing together in low areas inland, whereas *S. rubra* was found only along the margins of bayous. Several other putative hybrids between these species were observed, and certainly would be expected where related species grow in such close proximity. That the species remain as distinct as they are in the absence of geographical barriers is even more remarkable. It was thought that chromosome counts together with studies of chromosome morphology might indicate the relationships of these species and serve as a basis for an understanding of the possible mechanisms of speciation.

Root tips collected from plants of these six species and the one putative hybrid were fixed in a Navashin's fixative and embedded in paraffin following an ethyl-alcohol-chloroform series. Transverse sections were cut at 15  $\mu$ , and stained in accordance with a modification of the iodine-crystal-violet technique. The root tips of *S. rubra* were collected along the bayou between

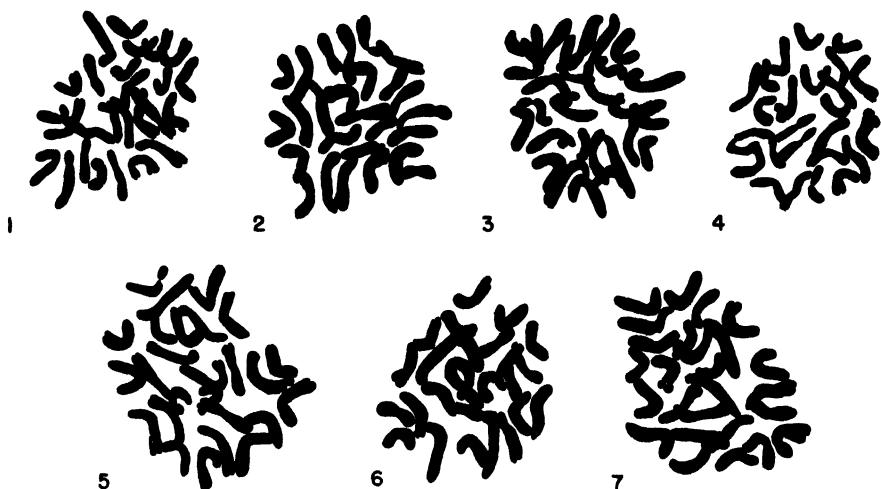
<sup>1</sup> Probably the northern variety, *S. purpurea* var. *gibbosa* (Raf.) Wherry.

<sup>2</sup> *S. variolaris* Michx. is now called *S. minor* Walt.

<sup>3</sup> The southern variety, *S. purpurea* var. *venosa* (Raf.) Wherry.

Valparaiso and Niceville, Florida; those of all of the other species and of the intermediate form were collected along Florida Highway No. 54, about three miles south of Crestview, Florida.

Karyotypes of root-tip metaphases are illustrated in figures 1-7. The chromosomes were drawn with the aid of a camera lucida at an initial magnification of 2825. The average diameter of each of the figures is approximately  $11\ \mu$ . The  $2n$  chromosome number proved to be 26 for all the material examined, but as the drawings show, the size and shape of the chromosomes provide little information concerning interspecific homologies. Although these counts do not agree with the two previous reports of chromosome numbers in *Sarracenia* cited above, it is entirely possible that



FIGS. 1-7. Karyotypes of root-tip metaphases of *Sarracenia*. FIG. 1, *S. purpurea*. FIG. 2, *S. psittacina*. FIG. 3, *S. rubra*. FIG. 4, *S. jonesii*. FIG. 5, *S. flava*. FIG. 6, *S. drummondii*. FIG. 7, putative hybrid of *S. flava*  $\times$  *S. drummondii*.

this earlier work is also correct, that different collections of a single recognized species may differ in chromosome number. On the other hand, aneuploid differences between closely related species and varieties are rare. Nichol's (1908) drawings show that she missed a few of the 12 pairs in some of the metaphase figures; it is possible that one of the pairs was obscured in the figures which she thought were complete.

The material for the present study was collected during World War II while the writer was stationed at an army air base in northwestern Florida. Since he is now located far from that area it is hoped that the publication of these observations may suggest a more thoroughgoing study of the cytological features of the *Sarracenias* to someone now working in the region where these plants grow.

## SUMMARY

The somatic chromosome number of *S. purpurea*, *S. psittacina*, *S. drummondii*, *S. flava*, *S. jonesii*, *S. rubra*, and of a putative hybrid of *S. drummondii* and *S. flava* was found to be 26. Previous counts for two of these species, *S. purpurea* and *S. rubra*, and a third not involved in the present study have been reported as  $n = 12$ .

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## A NOTE ON SARRACENIA

W. H. CAMP

The foregoing paper by Adolph Hecht on "The Somatic Chromosomes of *Sarracenia*" is of considerable interest to one working on biosystematic problems. In the second paragraph of this paper he states (and rightly) that it is not at all unusual to find a series of species of this group, as usually recognized, growing in the same area under fairly comparable conditions. In the same place intermediates and putative hybrids are noted; he adds: "That the species remain as distinct as they are in the absence of geographical barriers is even more remarkable." Since (as he modestly hints) these observations were made at a time when he was necessarily occupied with things of greater moment and so could not extend his investigations beyond a few localities, it will, I trust, be clearly understood that the following remarks are in no way intended as criticism of his observations. What he said about the apparent distinctness of these forms can be quite true in local areas. More extended observations doubtless would have led him to a somewhat different view of the "distinctness" of the Gulf Coast *sarracenias*.

My own work on various plant groups within this area was interrupted by the war; more recently it has been revived. In the Spring of 1948 I was studying the genic composition of certain plant populations along the Gulf Coast and, purely by accident, my itinerary included the localities mentioned by Hecht. Although my work was not directly concerned with the *Sarracenias* of the region, it would have indeed been difficult not to take considerable notice of these spectacular plants. The latest of these field studies, extending from the Florida east coast into Louisiana, gave opportunity to examine reasonably large populations of these plants.

On earlier excursions I had noted considerable variation; on the most recent trip the thing which renewed my interest in this group was the apparently large amount of genic introgression which had taken place between these various forms, not only locally but over a wide area. It was the *lack* of distinctness between these so-called species of *Sarracenia* which impressed me rather than the ease with which they could be separated. The number of named "hybrids" in this group is a hint that they are not genetically disjunct; and the series of subspecific "entities" recognized by various authors is further indication (as in so many other groups of plants) of the presence of an interlocked gene complex. With nothing reliable on

the cytology of this group available, it was impossible to proceed with any population studies beyond mere tentative observations.

It has become increasingly obvious that the taxonomy of a variable group containing a proportion of segregative polyploids must be approached in a different manner from that of one made up of homoploids capable of genic introgressions. As Hecht suggests, additional cytological study will be necessary to obtain a complete picture of the group. The great value of his preliminary paper lies in a demonstration of the homoploid condition of the series of materials on which his study was made; and these, apparently by accident, from what I consider to be one of the more critical areas. With this important information at hand, work now can proceed on the analysis of populations in this group by anyone interested with considerably greater assurance that the ultimate conclusions on its systematics will be sound. It is a great stride forward in our understanding of the rather complicated situation which one sees in the Gulf Coast *Sarracenia*s as demonstrated by what we now have adequate reason to suspect is no more than a series of genic introgressions on the homoploid level.

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## THE PROPAGATION OF *KALMIA LATIFOLIA* FROM SEED

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Within the horticultural trade *Kalmia latifolia* L. is considered to be one of the most difficult plants to propagate from seed and attempts to utilize cuttings have been unsatisfactory. The thousands of plants of this species sold annually are pillaged from native woodland stands either as mature specimens or as seedlings requiring a subsequent period of culture in the nursery. A successful and practical method of propagation of *Kalmia* from seed would not only make this popular plant available at more reasonable prices but also would preserve it in its natural plantations.

Rayner's studies (4) on the significant role of root-fungi in *Calluna* and related genera and Barrows' investigations (1) on the endophytic fungus found in *Epigaea repens* L. indicate that a mycorrhizal association is an important factor in the physiology of the *Ericaceae* under natural woodland conditions. In view of this it seems evident that any successful technique for the propagation of *Kalmia* from seed, either in the laboratory or in the nursery, must include consideration of the role of the mycorrhizal fungus always found in the roots of the wild plants. Rayner also states that in *Calluna* (4) the endophyte is not restricted to the roots but extends to all parts of the plant as well. If this were also true of *Kalmia*, the seed presumably would carry the mycelium of the endophytic fungus, the mycorrhizal association would thus begin under natural conditions at seed-germination, and there would be no need to supply the root-endophyte to the cultures at the time of germination of the seed. Attempts to demonstrate the presence of a fungus within the integuments of the ovules were unsuccessful and immature embryos removed under sterile conditions and planted in a medium suitable for the culture of plant embryos developed beyond the seedling stage entirely free from any associated fungus. This fact was substantiated by the absence of any fungal associate in all plants in sterile culture derived from surface-sterilized seed. It is apparent, therefore, that the mycorrhizal endophyte must be supplied artificially to secure a normal growth of the young *Kalmia* plants in a culture medium not enriched with organic compounds and growth substances. Furthermore, attempts to propagate *Kalmia* from seed, even in nursery beds specially prepared with soil from native stands, are usually unsuccessful. Although such beds presumably contain the mycorrhizal fungus associated with *Kalmia*, before the association can be effected, competitive fungi pathogenic to *Kalmia* begin to operate. In such beds the loss of young

seedlings may be complete and as yet no uniformly successful method has been devised for carrying the seedlings through the critical young stages. The problem within the laboratory is obviously less difficult since methods based upon sterile technique can be employed. A laboratory technique for the propagation of *Kalmia* from seed necessitates (first) the isolation in pure culture of the endophytic fungus with which *Kalmia* is associated under natural conditions, (second) the selection of an enriched medium suitable for seed germination and for the subsequent growth of the seedling under sterile conditions, and (third) the establishment of the mycorrhizal relationship by the combination of the seedling and the fungus in a minimal medium. Such a technique then may be adapted to horticultural practice as in the case of the sterile culture of orchids from seed.

**The Isolation of the Mycorrhizal Endophyte.** In early October, specimens of *Kalmia*, ranging in size from seedlings to plants of flowering age, were collected from a number of localities in the vicinity of New Haven, Connecticut. Microscopic examination of the roots of these plants disclosed in all abundant hyphae sheathing the younger portions with frequent penetrations into the cortical cells. A number of young roots were rinsed in several changes of distilled water to remove all surface debris and then treated for ten minutes in a solution of calcium hypochlorite (6). The sterilizing solution used in this treatment, as well as later for the sterilization of the *Kalmia* seeds, consisted of equal parts of the commercial laundry bleach known as Clorox and water containing 5 drops of the detergent Aerosol (25%, O. T. Clear) to 100 cc. (2). The roots were then rinsed in several changes of sterile distilled water and plated out in standard petri dishes on Difco malt agar in two-thirds the prescribed concentration. In 4-5 days numerous fungal hyphae grew out from the surface of the roots and several days later these developed into mycelial growths of eight distinct types. The most frequently occurring type, which developed always later than the others, formed a somewhat dense, white felt of only moderately rapid growth. All eight types were isolated and maintained on the Difco malt agar medium in slant cultures at room temperatures, to be used later in the determination of the true endophyte.

**The Culture of Sterile Seedlings.** Mature seeds of *Kalmia*, collected in the late fall from various localities in the vicinity of New Haven, were freed from capsule-debris by screening and stored in closed containers in a refrigerator at 35° F. Numerous samples of these seeds were sterilized by the process described in connection with the isolation of the root-endophyte for periods ranging from 10 to 30 minutes. About 1 cc. of each sample of seed was placed in a small Erlenmeyer flask and covered with the "Clorox-

Aerosol" solution. The flask was shaken gently to insure uniform action of the sterilizing solution. During this process it was observed that the seed containing well developed embryos settled to the bottom of the flask and that the chaff and aborted seed remained at the surface or in suspension. At the termination of the sterilization-period the "Clorox-Aerosol" solution together with the extraneous material was decanted off. The seed was rinsed twice in sterile distilled water, taken up in a sterile pipette of the medicine dropper type and then deposited in small amounts on an agar medium in small petri dishes. The seed was then spread uniformly over the surface of the agar with a sterile platinum loop. The medium selected for the germination and subsequent growth of the seedlings was that used for the culture of the *Kalmia* embryos. It is a modification of the medium for the culture of roots developed by Robbins and Schmitt (5) and later used by Burkholder also for the culture of roots and by Castle for the culture of small embryos of *Capsella*. In its modified form it has the following composition.

Ca(NO <sub>3</sub> ) <sub>2</sub> · 4H <sub>2</sub> O A.R.	0.4800 gm.
MgSO <sub>4</sub> · 7H <sub>2</sub> O A.R.	0.0630
KNO <sub>3</sub> A.R.	0.0630
KCl A.R.	0.0420
KH <sub>2</sub> PO <sub>4</sub> A.R.	0.0600
Trace elements in parts per million (B-1, Mn-1, Zn-7, Cu-2, Mo-1, Fe-5)	
Sucrose A.R.	20.0000
Thiamin	.0001
Niacin	.0005
Pyridoxin	.0001
H <sub>2</sub> O distilled	up to 1 liter
Agar (Difco, Noble)	9.0000
pH adjusted to 4.8 with 0.1 N H <sub>3</sub> PO <sub>4</sub>	
Autoclaved for 15 minutes at 15 pounds of pressure.	

The cultures were maintained in a humidified chamber at 22° C and illuminated by two "daylight" 20-watt fluorescent lamps placed at a distance of 15 inches. Germination began in 9-10 days after sowing or about 2 weeks earlier than seed sown in specially prepared nursery beds. Seed treated for 10 minutes in the "Clorox-Aerosol" solution gave complete sterilization with a high percentage of germination and this period of sterilization was adopted for all subsequent seed treatment. Sterilization periods in excess of 20 minutes, however, resulted in progressively lower percentages of germination.

Vigorous seedlings showing the first true leaf were transferred to dishes containing freshly prepared medium. Subsequent transfers and replacements were made to provide a sufficient number of individuals of approximately uniform size and vigor for the study of the effect in a minimal medium of the combination with each of the eight fungi isolated from the

*Kalmia* roots. At the end of eleven weeks each of the selected seedlings had 6-7 leaves and a well developed root-system.

**The Combination of the Sterile Seedlings and the Root Endophyte in a Minimal Medium.** By means of sterile forceps the selected seedlings were transferred to 125 cc. Erlenmeyer flasks containing 50 cc. of the following medium.

$\text{NH}_4\text{NO}_3$	0.500 gm.
$\text{KH}_2\text{PO}_4$	0.200
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	0.400
$\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$	0.130
Trace elements in parts per million (B-1, Mn-1, Zn-7, Cu-2, Mo-1, Fe-5)	
Agar (Difco, Noble), washed in 10 changes, 500 cc. each, distilled water	9.000
$\text{H}_2\text{O}$	up to 1000.000 cc.
pH adjusted to 4.8 with 0.1 N $\text{H}_3\text{PO}_4$	
Autoclaved for 15 minutes at 15 pounds of pressure	

Combinations with the fungi isolated from *Kalmia* roots were made by planting small tufts of mycelium in close association with the roots of each seedling. Eight series of five flasks, each flask containing eight seedlings, were inoculated in this manner with each of the eight fungi. An additional series of five flasks containing sterile seedlings was reserved without inoculation for comparison as controls. At the end of three weeks the inoculated seedlings exhibited marked differences when compared with those of the control series. In four series, through the pathogenic effect of the fungi the seedlings were either dead or in a dying condition. In three others the plants appeared to be in good condition and some showed a slight increase in growth over that of the controls. In the single remaining series, however, the seedlings were not only larger than the controls but of a deeper green color, indicating a definitely beneficial effect from the association with that particular fungus isolate. It is significant, moreover, that this isolate was the one most frequently obtained from *Kalmia* roots after sterilization of the root surface. At the end of three months these plants were 3-4 times larger than the controls and had maintained the deeper green color.

At this time the entire root system of one plant from each flask of this series was washed, fixed in a combination of chromic and acetic acids of medium strength, and stained with Orseillin BB and Crystal Violet according to the technique of Cohen and Doak (3). The preparations showed abundant hyphae on the root surface and frequent hyphal connections with mycorrhizal coils within the cortical cells. Microscopic observation of subsequent combinations of this fungus with *Kalmia* seedlings in a minimal

medium showed that extensive penetration of the mycorrhizal associate usually did not occur during the first three or four weeks of the association of the seedling and the endophyte. The remaining seedlings were then transferred to small pots containing a mixture of loam, sand and humus to which was added peat moss in sufficient quantity to secure the low soil pH required by *Kalmia*. The plants quickly became established and, after a month of growth in the open pots in the greenhouse, were upon an average approximately three times larger than the few *Kalmia* seedlings of comparable age surviving in seed-beds in the nursery.

#### SUMMARY

1. All roots of wild *Kalmia latifolia* examined showed the presence of mycorrhizal fungus both endotrophic and ectotrophic.

2. The mycorrhizal associate has been isolated and grown on a synthetic medium.

3. Sterile seedlings have been grown through early stages in a synthetic medium enriched with sucrose and growth substances.

4. The sterile seedlings when combined with the fungal associate on a minimal medium rapidly outgrew controls as well as seedlings of a comparable age which survive in nursery beds.

5. The results suggest the possibility of perfecting a culture technique for *Kalmia latifolia* comparable with the technique commonly employed for orchids.

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## A REINVESTIGATION OF THE EMBRYO SAC OF *MAIANTHEMUM CANADENSE*

B. G. L. SWAMY

McAllister's (1914) report of the occurrence of an *Adoxa* type of embryo sac in *Maianthemum canadense* was taken for granted to be the true situation until Stenar (1934) found the *Drusa* type of development in *M. bifolium*. This conflict of reports for *Maianthemum* and the fact that in recent years several of the alleged *Adoxa* types are proving to be different upon reinvestigation, urge a restudy of *M. canadense* (see also Maheshwari 1947a). The material for the present investigation was collected from the Arnold Arboretum of Harvard University.

The dyad nuclei resulting from the first meiotic division in the megaspore mother cell are separated by a wall (fig. 1). The second division results in four megaspore nuclei, each separated by a wall (figs. 2-4). The arrangement of the megaspores of the tetrad in the majority of ovules is tetragonal (figs. 2, 3) whereas a linear condition (fig. 4) is rather rare. In either case, the walls separating the megaspores are only transitory, and after a time the four nuclei lie in the common cytoplasm, enclosed by the original wall of the megaspore-mother cell (fig. 5).

Whatever is the type of arrangement of the megaspores in a tetrad, the nuclei become disposed in 1+3 arrangement before the next division (fig. 6). As a result of a simultaneous division of all the four nuclei (fig. 7), a 2+6 arrangement of the nuclei becomes established at the 8-nucleate stage (fig. 8). One more division of these nuclei (fig. 9) results in a 16-nucleate embryo-sac (fig. 10), with an egg apparatus of two synergids and an egg cell, 11 antipodal cells, and two polar nuclei.

It must be mentioned at this point that the number of antipodal cells frequently is less than eleven. In a small percentage of the sacs, this is brought about by the failure of division of one or more of the chalazal nuclei at the 2+6-nucleate stage, a situation comparable to that in *Ulmus* (D'Amato 1940; Ekdahl 1941). However, the predominant method of reduction in the number of antipodals is their very early degeneration. The antipodal cells at the farthest chalazal end appear to degenerate and disappear sooner than those that lie nearer to the center of the sac. In other words, the antipodals situated towards the interior of the sac are the last to suffer degeneration. As a result of these two phenomena (failure of division of the chalazal nuclei and early degeneration of antipodals) the embryo-sac at anthesis contains less than 16 nuclei. Although the number

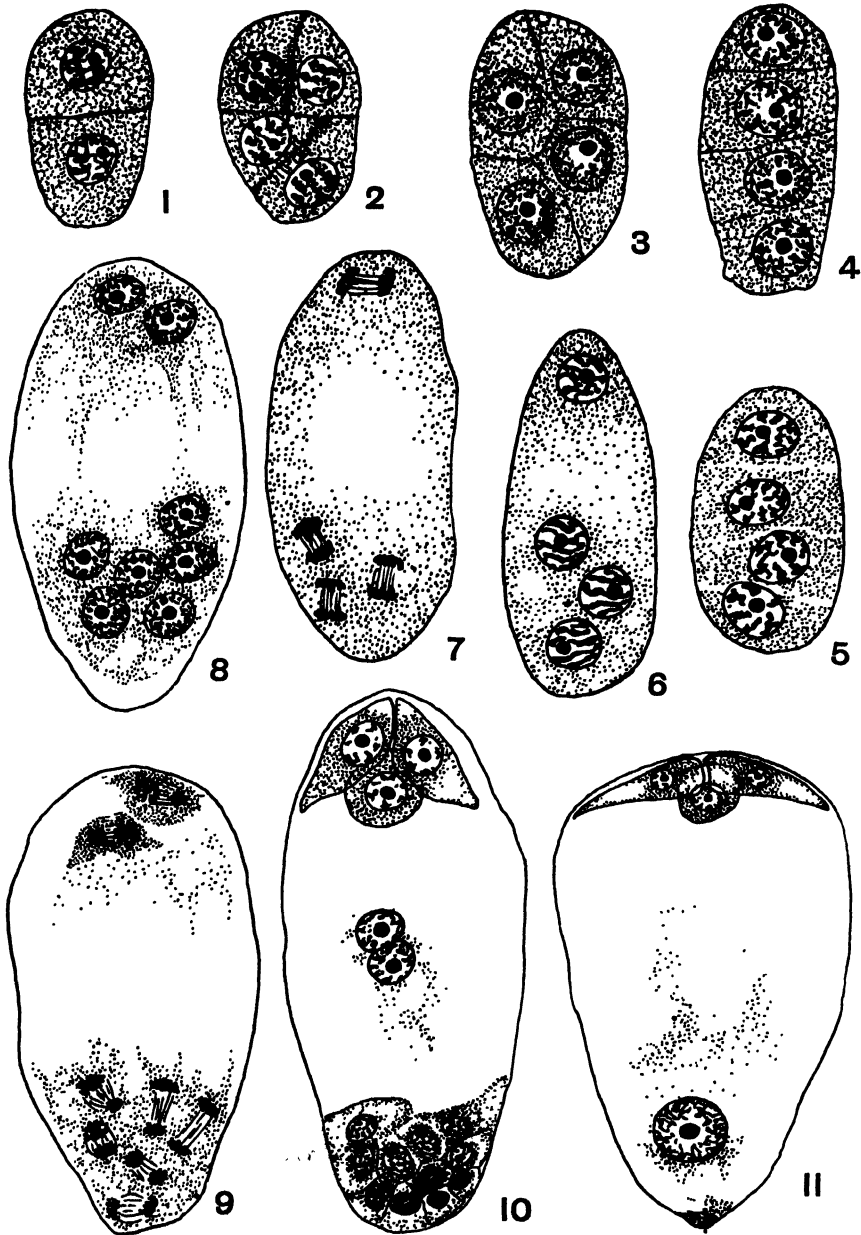


FIG. 1. Dyad stage. FIGS. 2-4. Tetrad stage. Note the transitory walls between the megaspore nuclei. FIG. 5. A linear tetrad after the dissolution of the walls separating the nuclei. FIG. 6. 1+3 arrangement of the megaspore nuclei. FIG. 7. Division of the megaspore nuclei. FIG. 8. 2+6-nucleate stage. FIG. 9. Final division of the gametophytic nuclei. FIG. 10. 16-nucleate embryo-sac soon after its formation. FIG. 11. Embryo-sac in which the antipodal cells have degenerated. All figures,  $\times 560$ .

of the persisting antipodal cells fluctuate widely—anywhere between 1 and 11—the most frequent range is between 2 and 4. Particularly in those embryo sacs that failed to receive the pollen tube at the right time, the only persisting structures are the egg apparatus and the secondary embryo-sac nucleus (fig. 11). This situation helps us to understand how McAllister overlooked the fundamental 16-nucleate nature of the embryo sac in *M. canadense*.

Of 373 embryo sacs examined, the development in 322 followed the method just described. In the remaining 51 the procedure is different. During the division following the 2 + 6-nucleate stage of the gametophyte (fig. 12), the metaphase spindles at the chalaza fuse in pairs, thereby resulting in six diploid nuclei at the corresponding end (figs. 13, 14). Although actual counting of the chromosomes on these spindles has not been possible, a complete series of stages in the derivation of the diploid nuclei has been observed. Furthermore, there are other evidences for the diploid condition of the chalazal nuclei: the larger breadth of the chalazal spindles during the early stages of fusion as compared with those of the micropylar end (fig. 12); the corresponding relation maintained by the resulting nuclei during the telophase of the same division (fig. 13); the larger size of the chalazal nuclei each containing two distinct nucleoli, as compared with the smaller nuclei each with a single nucleolus at the micropylar end; the richer accumulation of chromatin material of the chalazal nuclei in contrast to the micropylar group after the division (fig. 14). One of the diploid nuclei functions as the antipodal polar nucleus (fig. 15). Under these circumstances, the mature embryo-sac is 10-nucleate—four haploid nuclei at the micropylar end and six diploid nuclei at the chalazal end. The antipodals organize into cells as in the typical 16-nucleate sac.

This second type of development is particularly interesting. That the Drusa and Fritillaria types occur in the same species in varying proportions is especially revealed in *Tamarix* (Battaglia 1941). In *T. africana*, Battaglia finds the Fritillaria type in 43 per cent of the ovules and the Drusa type<sup>1</sup> in 57 per cent. That these two types are closely related is becoming increasingly evident (see Maheshwari 1947 a, b). In *T. africana*, the commoner Drusa type of development switches over to the less common Fritillaria type at the 1 + 3-nucleate stage and the resulting chalazal nuclei are triploid. On the other hand, in *M. canadense*, the fusion is carried over to the 2 + 6-nucleate stage and as the spindles fuse in pairs, the resulting nuclei are diploid. Although this situation may not strictly fall within the true Fritillaria type, the general trend of the process is obviously similar, and therefore may still be looked upon as a variant of the Fritillaria type.

<sup>1</sup> Battaglia refers these to the Pyrethrum type; however, I am in agreement with the views expressed by Maheshwari (1947 b, p. 19) in amalgamating this with the Drusa type.



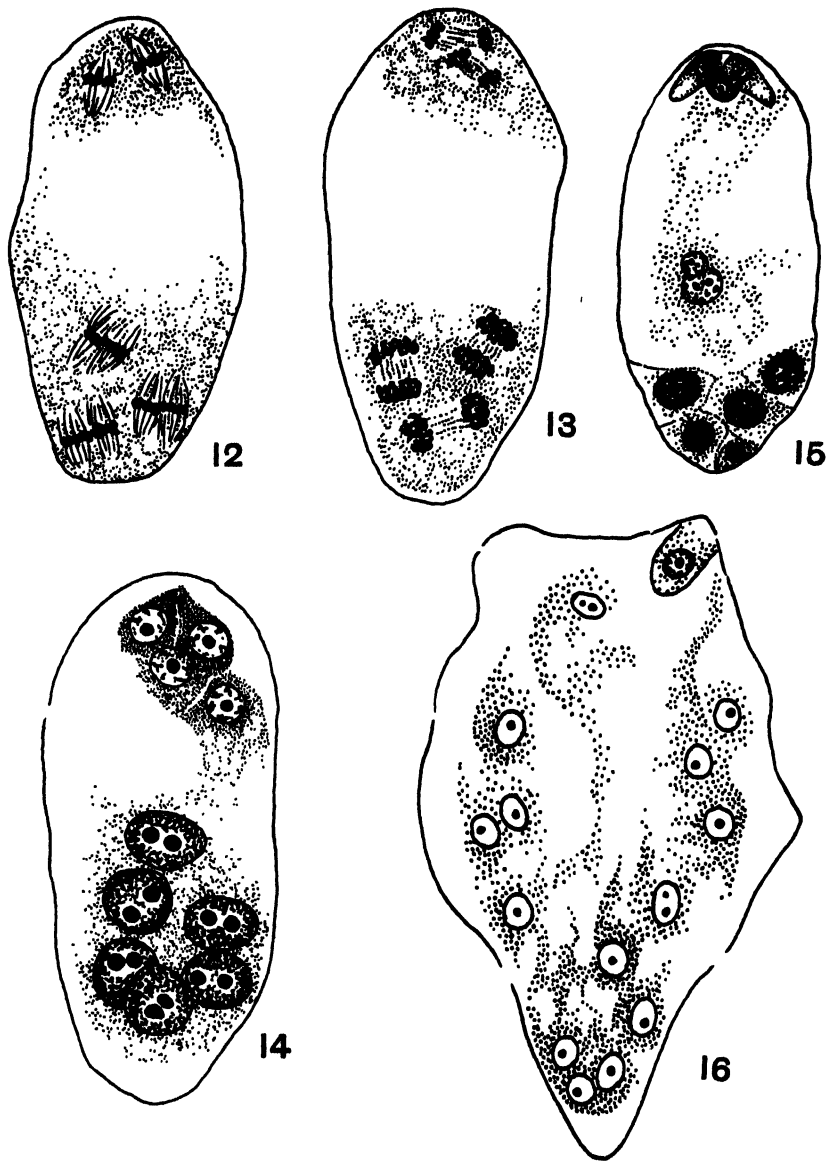


FIG. 12. Metaphase during the division of the nuclei following the 2+6-nucleate stage. Note the chalazal spindles fusing in pairs. FIG. 13. The same, telophase. Note the larger size of the nuclear masses on the chalazal spindles. FIG. 14. Slightly later stage than in figure 13: The four haploid nuclei at the micropylar end are organizing into the egg apparatus and the polar nucleus of the corresponding end and the six diploid nuclei at the chalazal end are not yet differentiated as cells. FIG. 15. Mature organization of the embryo-sac following the stage depicted in figure 14. FIG. 16. Zygote and free nuclear endosperm. Figs. 12-15,  $\times 560$ ; Fig. 16,  $\times 300$ .

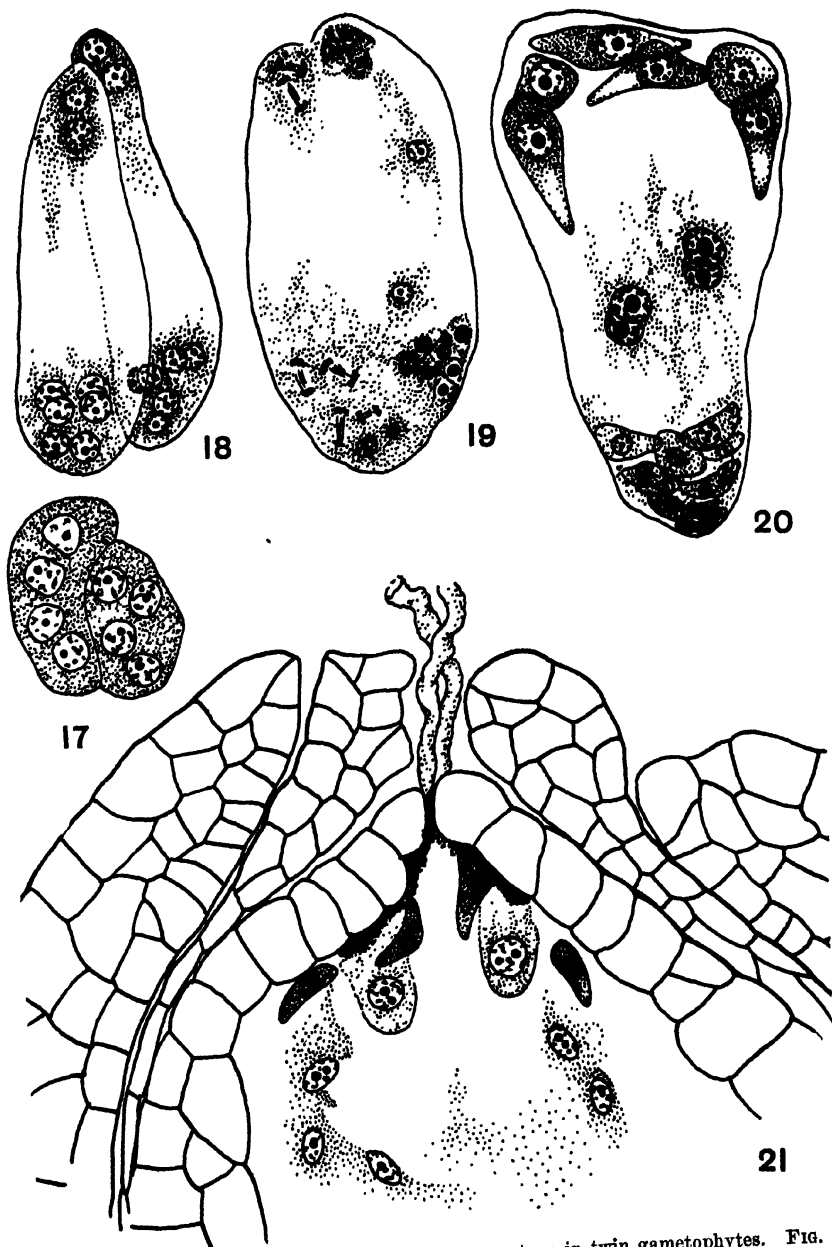


FIG. 17. Twin tetrads. FIG. 18. 2 + 6-nucleate stage in twin gametophytes. FIG. 19. Final division of the nuclei in one gametophyte and the beginning of organization of the nuclei in the other. The contiguous walls of the gametophytes are broken down. FIG. 20. Mature "compound" embryo-sac. FIG. 21. Post-fertilization stage of an embryo-sac as illustrated in figure 20, showing the integuments, the entry of two pollen tubes, the persistence of four synergids, two zygotes, and free nuclear endosperm. Figs. 17-20  $\times 560$ ; Fig. 21,  $\times 300$ .

In the fully mature embryo-sac, the secondary embryo-sac nucleus characteristically occupies a position nearer to the antipodals (fig. 11). Double fertilization takes place and the primary endosperm nucleus builds up free nuclear endosperm (fig. 16). The same condition is described in *M. bifolium* (Stenar 1934).

In *M. bifolium* Stenar (1934) records the occurrence of two megasporophyte cells side by side. This occurs in the species studied at present also. Furthermore, both of them undergo more or less simultaneous development and develop into mature embryo-sacs, following the Drusa type (figs. 17-19). After the 2+6-nucleate stage, the contiguous walls of the twin gametophytes break down (fig. 19) and thus the resulting structure contains two sets of egg apparatus at the micropylar end, two sets of polar nuclei in the center and a varying number of antipodal cells at the chalazal end (fig. 20). Only one instance of such a "compound" embryo-sac being fertilized by two pollen tubes was observed and this is illustrated in figure 21. As there is definite evidence of two pollen tubes having entered the gametophyte and as both the zygotic nuclei show two nucleoli, it is to be assumed that each pollen tube has fertilized an egg. All the four synergids may be seen lying about the zygotes. This situation is a clear example of one method of the origin of polyembryony.

#### SUMMARY

A reinvestigation of the embryo-sac of *Maianthemum canadense* shows that it follows the Drusa type but not the Adoxa type as was reported by McAllister. However, all the 11 antipodal cells are not often in evidence at the mature condition owing to the early degeneration of several of them and also due to the failure of division of some of the chalazal nuclei during the preceding stages.

In about 13 per cent of the ovules, during the division following the 2+6-nucleate stage, the chalazal spindles fuse in pairs so that the mature gametophyte comes to possess four haploid nuclei at the micropylar end and six diploid nuclei at the chalazal end. In view of the close inter-relationships existing between the Drusa and Fritillaria types, it is suggested that this peculiar variation may be interpreted as a belated tendency to switch over to the Fritillaria type.

The development of twin embryo-sacs and their ultimate fusion into a "compound" structure and the actual fertilization of both the egg apparatus by two pollen tubes is demonstrated.

I express my appreciation to Miss Charlotte S. Pratt for the help she rendered in the preparation of this paper.

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**CORDYCEPS BICEPHALA BERK. AND C. AUSTRALIS (SPEG.)  
SACC.<sup>1</sup>**

E. B. MAINS

Recently several collections of a *Cordyceps* infecting ants were received from Liberia from J. T. Baldwin, Jr. who states that it is a common parasite there, killing ants by the thousands in the Western Province. The specimens have clavae which are bicolored, dark purplish-brown below and light brownish-yellow to cream-colored above. The stipes are slender and are terminated by ovoid to ellipsoid heads. Most of the clavae are simple (figs. 3, 4). In one specimen (fig. 1) the stipe is furcate and two heads were formed. The perithecia are entirely embedded in the head and are oblique, overlapping each other upward (fig. 2). In many collections the infected insects are attached to stems of plants, gripping them with their mandibles and legs.

Several species of *Cordyceps* on ants have been described with bicolored clavae. *Cordyceps proliferans* P. Henn. on an ant from South America is illustrated (3) as having furcate clavae, cylindric heads, and ovoid perithecia embedded at right angles to the surface of the head. The asci are described as cylindric-clavate,  $150-180 \times 4-5 \mu$ . Hennings (4) also described another bicolored species, *C. Huberiana*, on an ant from South America. The clavae apparently are simple, the fertile portions cylindric, 8-9 mm. long and 1 mm. thick, the perithecia oblong, completely embedded, and the asci cylindric,  $150-200 \times 5-6 \mu$ . The furcate condition of the clavae appears to be the principal distinction between *C. proliferans* and *C. Huberiana*. As Petch (12) has concluded, they apparently are the same species. The Liberian collections differ in the ovoid to ellipsoid heads, the oblique perithecia, and much longer asci.

*Cordyceps necator* was described by Patouillard and Hariot (10) as having bicolored clavae on ants from French Guinea. The specimens were immature and information is not available concerning the perithecia and asci. The application of the name is uncertain.

In 1882 Spegazzini (15) described a bicolored *Cordyceps* on an ant from Brazil under the name *Cordyceps* (*Torrubia*) *unilateralis* Tul. *australis* Speg. In 1883 Saccardo (14) raised it to specific rank. The fertile portions of the clavae are described as elliptic-subglobose or subovate, the perithecia

<sup>1</sup> Paper from the Herbarium and the Department of Botany of the University of Michigan.

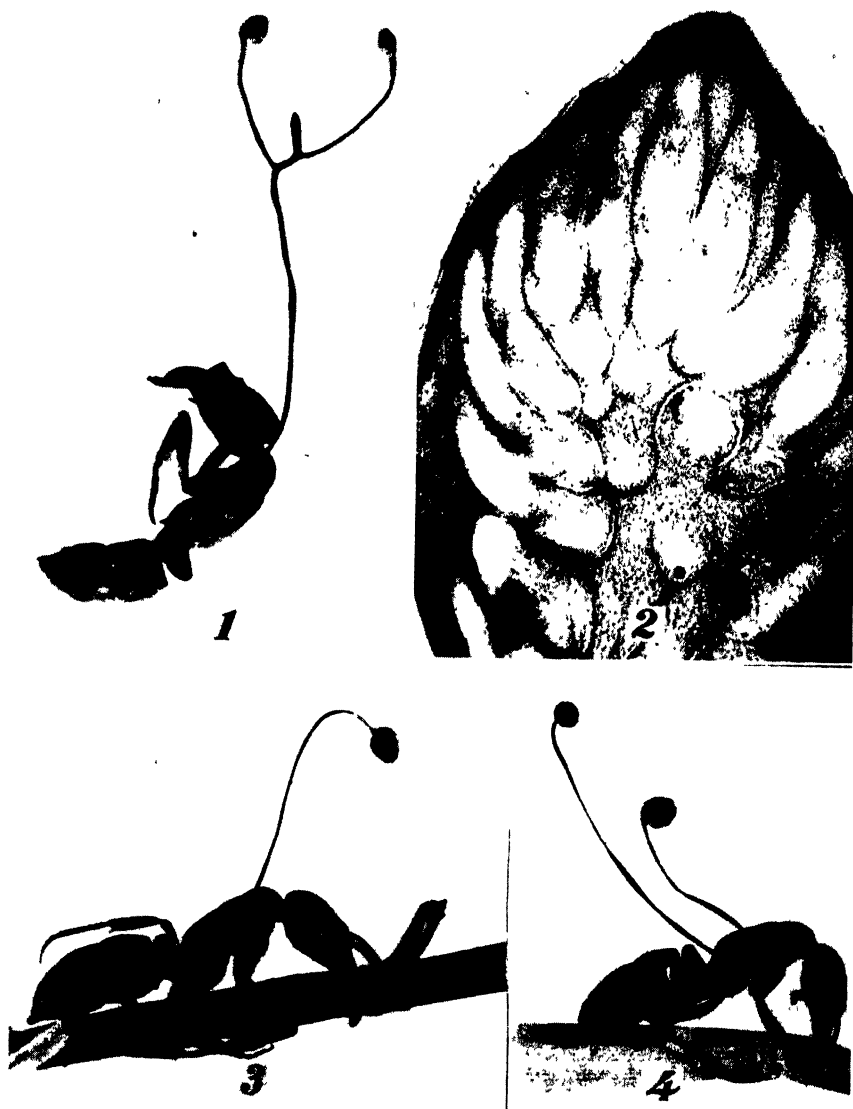


FIG. 1. Ant with a furcate clava of *Cordyceps australis* terminated by 2 heads, collected by J. T. Baldwin Jr. (10480), Western Province Liberia.  $\times 3$ . FIG. 2. Longitudinal section through a head of *Cordyceps australis* showing the oblique, overlapping perithecia.  $\times 45$ . FIG. 3. Ant with a single clava of *Cordyceps australis* arising from the thorax, collected by J. T. Baldwin Jr., Western Province Liberia Dec. 1947.  $\times 3$ . FIG. 4. Ant showing two clavae from the same collection as 3. The bicolored condition of the clavae does not show due to printing to obtain contrast with the background.

as completely embedded, and the asci as cylindric,  $240\text{--}250 \times 4\text{--}5 \mu$ . The orientation of the perithecia is not given. Later Spegazzini (16) again described the species, giving beetles as well as ants as hosts. Möller (9) reported a *Cordyceps* as *C. australis* from Brazil. In his description of the collections he emphasized the orientation of the perithecia which are described as flask-shaped,  $650\text{--}750 \times 250 \mu$  and arranged like scales in a cone i.e. oblique to the surface and overlapping upward. The asci are described as up to  $700 \mu$  long, which is considerably longer than the measurements given by Spegazzini. The Liberian specimens agree very well with the description as given by Möller. The question however arises whether Möller's material is *Cordyceps australis*, since he apparently had not studied the collections described by Spegazzini.

Through the kindness of Juan C. Lindquist the collections in the Spegazzini Herbarium of *Cordyceps australis* were loaned for study. The outer envelope containing specimen 1768 has the following data "*Cordyceps unilateralis australis* Speg. Typus! *Pachycandyla striata* Apiahy (Brasil) leg. Puiggari". An inner envelope bears sketches apparently by Spegazzini of a section of a head, perithecia, asci, and spores. The perithecia are drawn as oblong, slightly oblique, and measurements of  $500\text{--}600 \times 100 [\mu]$  are given. The asci are drawn as narrowly cylindric with the wall thickened at the apex, and measurements of  $400\text{--}450 \times 7\text{--}8 [\mu]$  are given. The ascospores are illustrated as filiform, multiseptate,  $250 \times 2 [\mu]$ , and the part-spores as fusoid cylindric,  $10\text{--}15 \times 1\frac{1}{2}\text{--}2 [\mu]$ . It should be noted that these data do not agree with those given in the description published by Spegazzini (15). The specimen now consists only of portion of a purplish-brown stipe attached to a curculio beetle.

The outer envelope of specimen 1769 has the following data "*Cordyceps australis* Speg. Apiahy (Brasil) leg. Puiggari no. 2335." The inner envelope has the notation "immatura" and now contains only two fragments of purplish-brown stipes and portions of a beetle.

The outer envelope of specimen 1770 bears the following data, "*Cordyceps australis* Speg. Apiahy (Brasil) leg. Puiggari." On the inner envelope is written, apparently by Spegazzini, *Cordyceps unilateralis* Tul. (sub *Torrubia*) with *unilateralis* crossed out and *australis* written underneath. Additional data are as follows "in formica Apiahy, Brasilia meridionali leg. Puiggari." There are also the notations "(+ *Cordiceps curculionum* ?)" and "an *C. bicephala* Berk.?" There are several sketches. One shows a clava with a slender stipe arising from between the head and thorax of an ant and terminating in an ovoid head. About half way on the stipe is a lateral globoid swelling. The asci are shown as cylindric with measurements  $240\text{--}250 \times 4\text{--}5 [\mu]$ . The part-spores are cylindric, rounded at the ends, with measurements  $5\text{--}10 \times 1 [\mu]$ . The data and sketches agree closely

with the description as first published by Spegazzini (15). It seems fairly certain that no. 1770 is the type specimen of *Cordyceps australis* (*C. unilateralis australis*). The envelope contains fragments of both ants and beetles. There are several fragments of stipes which are dark purplish-brown below and brownish- or reddish-yellow above. One stipe has a lateral sterile swelling like that shown in the sketch. Only one head occurs in the collection and it is glued to a piece of paper. A portion had been removed. It apparently was narrowly ellipsoid,  $2 \times 1$  mm. It was possible to remove a few perithecia for study. The perithecia are conoid,  $770\text{--}880 \times 230\text{--}250 \mu$ . They are arranged obliquely, overlapping upward. The asci are narrowly cylindric,  $4\text{--}5 \mu$  wide and up to  $600 \mu$  long. The wall of the ascus is thickened at the apex up to  $4\text{--}5 \mu$ . The ascospores are filiform, multiseptate breaking into fusoid-oblong, one-celled fragments,  $8 \times 1.5 \mu$ .

Both no. 1768 and 1769 are *Cordyceps curculionum* Tul., a parasite of beetles. It is not surprising that Spegazzini included the fungi on ants and beetles under one species since they are very similar and evidently closely related. *C. curculionum* has bicolored clavae, ovoid to ellipsoid heads, oblique perithecia entirely embedded and overlapping upward, and cylindric asci,  $400\text{--}480 \times 6\text{--}8 \mu$ . *C. curculionum* is somewhat more robust than the fungus occurring on ants and the asci are wider. The differences are not great and a specific separation may well be questioned. However for such parasites it seems logical to recognize specific separations based on the parasitism of two such distinct host groups as the beetles and the ants. The question whether the name *Cordyceps australis* should apply to the beetle or ant fungus is difficult to answer. If Speg. Herb. no. 1768 labeled Typus is considered the type, the name applies to the beetle fungus on the basis of the data on the inner envelope and what is left of the specimen. If so, it would become a synonym of *C. curculionum*. However, as has been pointed out, Speg. Herb. no. 1770 apparently is the type of *C. australis*. The occurrence of both beetles and ants in the packet indicates that both fungi may have been included in the original description. The specimens are in fragments and it is impossible to determine host connections. However the data obtained from the only head left in the collection indicates that it belongs to the ant fungus since it contains narrow asci. Also the sketch made by Spegazzini shows the fungus arising from an ant and the data he gives apparently were obtained from the ant fungus. It therefore seems safe to conclude that the name *C. australis* should be applied to the species on ants. With this interpretation the Liberian collections are *C. australis*.

Spegazzini (16) described another bicolored species on ants *Cordyceps goniophora*. Petch (13) has considered this a synonym of *C. Humberti*. A study of the type (Herb. Speg. 1779) has resulted in the conclusion that it is an immature specimen of *C. australis* in which poor conditions for growth or injury to the stipe have resulted in abnormal development of the clavae.



Spegazzini (15), following his description of *C. unilateralis australis*, raised the question whether it might be *C. bicephala*, Berk. Berkeley (1) describes the single clava as brown and furcate with two elliptical heads. The host is not given and probably was not collected. Cooke (2), Massee (8), and Lloyd (6) have discussed the species, apparently entirely from the type specimen. The orientation of the perithecia is not described and the only indication of a bicolored condition is Massee's statement that the stem is brown, paler upward. Petch (11) has concluded that *C. australis* is a synonym of *C. bicephala*. In his discussion of the species, he describes a bicolored condition but does not give the orientation of the perithecia. It is not clear how much of his data are derived from the type and how much from later collections which were determined as *C. bicephala*.

In answer to a request for information concerning the type in the Kew Herbarium Miss E. M. Wakefield writes that the type specimen of *C. bicephala* now consists of a single stalk forked at the top, originally bearing a head on each branch. Only one head is still attached. The other has been used for examination and is included in a small packet. The stalk is dark brown to black below. The upper part of the stem and the branches are buff or alutaceous. She loaned a slide having sections of the detached head. The perithecia were found to be conoid,  $580-630 \times 160-200 \mu$ , and arranged obliquely, overlapping upward. It was not possible to distinguish asci and ascospores. This would support the decision of Kabayasi (5) that the name should be excluded as based on an immature specimen. Berkeley (1) describes asci stating that they are linear with clavate tips and the spores as very slender and linear. Massee (8) gives the asci as cylindric and capitate and the spores as linear  $70 \times 1 \mu$ , multiseptate and the cells as  $3 \mu$  long. His measurements do not agree with those of *C. australis*. It seems doubtful whether the name *C. bicephala* can be used with certainty. A tendency toward a bicephalate condition has been noted for the ant fungus by Spegazzini, Möller, and Petch and one of the Liberian specimens shows it. However, furcate clavae occasionally occur in a number of species of *Cordyceps*. With the host unknown and data concerning the asci and ascospores insufficient it is not possible to determine whether the name *C. bicephala* should apply to *C. australis* or *C. curculionum*. It therefore seems best to consider it of doubtful application. The objection can be raised that *C. australis* was based on a mixed collection. The evidence indicates that the description was based on the ant fungus and therefore it is accepted instead of proposing a new name which otherwise would be necessary. The following description is based on collections from the Farlow Herbarium, Harvard University,<sup>2</sup> the

<sup>2</sup> The writer is indebted to Rolf Singer and W. Lawrence White of the Farlow Herbarium, D. P. Rogers of the Herbarium of the New York Botanical Gardens and Juan C. Lindquist of the Museo de la Plata for the loan of specimens for this study.

Herbarium of the New York Botanical Garden, the Spegazzini Herbarium, and the Herbarium of the University of Michigan.

*CORDYCEPS AUSTRALIS* (Speg.) Sacc. Syll. Fung. **2**: 571, 1883. *Cordyceps unilateralis australis* Speg. An. Soc. Cien. Argent. **13**: 215, 1882. *Cordyceps gomophora* Speg. Bol. Acad. Nac. Cien. Cordoba **11**: 540, 1889.

Clavae one or two arising from the thorax of an ant, simple or occasionally furcate, 10–25 (65) mm. long, the stipes very slender 0.2–0.3 mm. thick, dark purplish-brown to brownish-black below, light yellowish-brown to cream-color in the upper one-third, probably some shade of red when fresh, occasionally producing short sterile side branches or equally branched with terminating heads, capitate, the heads ovoid, ellipsoid or obovoid, 1.5–3 × 0.5–1.8 mm. smooth to somewhat rugose in the lower part, punctate from the ostioles of the perithecia, concolorous with the upper part of the stipe; perithecia entirely embedded, oblique, overlapping upward, conoid, 720–960 × 230–336  $\mu$ ; asci cylindric, 500–720 × 4–5  $\mu$ , the wall thin, thickened over the apex, 4–6  $\mu$ , the ascospores filiform, multiseptate, breaking into one-celled part-spores, fusoid-cylindric, slightly narrowed and rounded at the ends, 6–10 × 1–1.5  $\mu$ .

On several species of ants.

BRAZIL: Apiaby, *J. Puiggari*, (Herb. Spegazzini 1770); Apiaby, *J. Puiggari*, 1881, (Herb. Spegazzini 1779); Tijuca, vicinity of Rio de Janeiro, *J. N. Rose & P. G. Russell*, (N. Y. Bot. Gard. 21192). BRITISH GUIANA: Tumatumari, Sept. 19, 1923, *D. H. Linder* 210 (Farl. Herb.); Tumatumari, Sept. 20, 1923, *D. H. Linder* 211 (Farl. Herb.); on *Paraponera clavata*, Bartica, Dec. 9, 1923, *D. H. Linder* (U. Mich.). LIBERIA: Gbanga, Sept. 15, 1926, *D. H. Linder*, (Farl. Herb.); Gbanga, September, 1926, *D. H. Linder* 270 A, (Farl. Herb.); Gbanga, September, 1926, *D. H. Linder* 395, (Farl. Herb.); Banta, 1939, *G. W. Harley* (Farl. Herb.); Zui, Western Province, Nov. 11, 1947, *J. T. Baldwin Jr.* 10480 (U. Mich.); route Belleyella—Kondessu—Zui—Genne, Western Province, Dec. 1947, *J. T. Baldwin Jr.* (U. Mich.); Bonata, Central Province, Dec. 8, 1947, *J. T. Baldwin Jr.* (U. Mich.).

TYPE specimen on *Pachycondyla striata*, collected by *J. Puiggari*, Apiaby Brazil (Herb. Speg. 1770), Museo de la Plata, Argentina.

According to Petch (11) the conidial stage of *C. australis* was found on specimens collected by Paul W. Richards in British Guiana. It may arise as a branch of the perithecial clava or as an independent linear clava. He considers it to be the same as *Isaria melanopus* Speg. and states that it belongs in *Hymenostilbe*. He makes the transfer proposing the name *Hymenostilbe melanopoda* (Speg.) Petch (*H. melanopus* Mains, 7). Spegazzini (16) described *Isaria melanopus* from a collection on beetles and suggested that it was the conidial stage of *Cordyceps australis*. However, as has been pointed out Spegazzini considered that *C. australis* occurred on both ants and beetles. Since *C. australis* on ants is recognized as a separate species from *C. curculionum* on beetles it would follow that *Isaria melanopus* is probably the conidial stage of the latter species. According to Petch the conidial stage of *C. australis* of Richard's collections has phialides which are ovoid, minutely verrucose at the apex, 7–9 × 4  $\mu$ , with a short

central truncate sterigma and conidia which are hyaline, fusoid, with a truncate base,  $7-9 \times 1 \mu$ .

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NEW SPECIES OF PUCCINIA ON LAURACEAE FROM CHINA<sup>1</sup>GEORGE B. CUMMINS<sup>2</sup>

The rusts reported below form a closely related series of species. The relationship is so close that it is difficult in some cases to decide specific limits.

It is essential that the telia be studied in section, since the species are divisible into three main groups depending upon the diameter of the sorus and its position relative to the tissues of the leaf. In the first group the telia are cup-shaped, with a diameter of 60–100  $\mu$ , and are seated next the palisade layer, thus deeply within the leaf tissue. In the second group the telia are likewise seated next to the palisade layer but have a diameter ranging from 100–175  $\mu$ . Measurements are given for the sorus proper since the spores, when extruded, overspread the leaf surface as a pulvinate cushion much exceeding the diameter of the sorus within the leaf. In the third group the sori are merely subepidermal, thus neither cup-shaped nor deep-seated, and usually exceed 200  $\mu$  in diameter. Here again, the spores overspread the leaf. Superficially, the sori of all groups appear to be similar and the exposed mass of spores is 0.5–1.0 mm. in diameter.

Part of the species have teliospores with uniformly thick side walls. In the remainder the side wall penetrated by the germ pores is usually conspicuously thicker than the rest of the wall. This unilateral thickening is often accompanied by a tendency to curvature away from the thickened side. This is especially conspicuous in *P. scimitriformis*.

Most of the teliospores have rugose walls but this may be so indistinct as to be of no real value in some species. Most germinate without a rest period. The germ pore is apical or nearly so in the upper cell while that of the lower cell is adjacent to the septum.

The following key is presented as an aid in differentiating the species described here:

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<sup>1</sup> Cooperative investigations between the Purdue University Agricultural Experiment Station and the Division of Mycology and Disease Survey, Bureau of Plant Industry, Soils, and Agricultural Engineering, United States Department of Agriculture. Journal Paper Number 344, of the Purdue University Agricultural Experiment Station. Contribution from the Department of Botany and Plant Pathology.

<sup>2</sup> The rusts reported in this paper were collected in cooperation between the Farlow Herbarium of Harvard University and the University of Nanking. They were made available for study through the courtesy of the late Dr. D. H. Linder. All specimens are deposited in the Arthur Herbarium, Purdue University and the Farlow Herbarium, Harvard University. Unless otherwise stated collections are by S. Y. Cheo.

Sori deep-seated, cup-like, next the palisade layer.

Sori 100  $\mu$  or less in diameter.

Side walls of teliospores uniformly 1.5–2  $\mu$ .

Teliospores ellipsoid, 15–20  $\times$  39–56 (–60)  $\mu$ .

*P. cinnamomicola*.

Teliospores cylindric, 10–19  $\times$  65–96  $\mu$ .

*P. seposita*.

Side walls of teliospores unilaterally thickened.

Teliospores broad, 14–20  $\times$  50–75  $\mu$ , nearly straight.

*P. morata*.

Teliospores narrow, 12–15  $\times$  60–83 (–90)  $\mu$ , curved.

*P. scimitriformis*.

Sori 100–175  $\mu$  in diameter.

Side walls of teliospores uniformly 1.5–2  $\mu$ .

Teliospores oblong-ellipsoid, 14–19  $\times$  47–60  $\mu$ .

*P. cara*.

Teliospores ellipsoid, 17–25  $\times$  45–72  $\mu$ .

*P. aequitatis*.

Side walls of teliospores unilaterally thickened; teliospores 17–22  $\times$  (53–) 57–86 (–92)  $\mu$ .

*P. machili*.

Sori not deep-seated, subepidermal, 200  $\mu$  or more in diam., side walls of teliospores uniform.

Teliospore wall obviously rugose-reticulate, spores 16–23  $\times$  (48–) 52–75  $\mu$ . *P. machilicola*.

Teliospore wall obviously verruculose, spores 22–26 (–29)  $\times$  43–55 (–60)  $\mu$ .

*P. coronopsora*.

Teliospore wall smooth, spores 13–17 (–19)  $\times$  (52–) 65–96 (–105)  $\mu$ .

*P. lauricola*.

***Puccinia cinnamomicola* Cummins, sp. nov.** (fig. 1). Spermatophytes non visis. Aecis sterilibus cellis consociatis usque ad 90  $\mu$  diam., ex cellulis peridioideis compositis; cellulis individuus 12–15  $\times$  14–20  $\mu$ , membrana 2.5–3.5  $\mu$  crassa, verrucosa. Uredii nullis. Teliis hypophyllis, in maculis brunneis leniter incrassatis circinater aggregatis, obscure brunneis, pulvinatis, profunde immersis, 80–100  $\mu$  diam.; teliosporis (fig. 1) ellipsoideis, utrinque rotundatis vel deorsum plus minusve attenuatis, medio constrictis, 15–20  $\times$  39–56 (–60)  $\mu$ ; membrana 2  $\mu$  crassa vel ad apicem usque ad 3.5  $\mu$ , aureo-vel cinnamomeo-brunnea, minuteque rugosa vel apparenter levi, poris germ. in cellulis superioribus apicalibus, inferioribus ad septum dispositis; pedicello hyalino, tenui, 3  $\mu$  crasso, usque ad 200  $\mu$  longo, tenuiter tunicato, fragili. Statim germ.

On *Cinnamomum* sp. KWANGSI PROV: Ta Tseh Shan, YUNG HSIEN, Aug. 22, 1933, *Cheo 2557* (TYPE).

Because of the presence of sterile aecia composed of compacted cells, which apparently are non-functional, this rust could doubtless be placed in the genus *Xenostele*. In *X. litseae* (Pat.) Syd. and *X. echinacea* (Berk.) Syd., however, the teliospores develop in the base of the aecial peridium. This is not true of *Cheo*'s collection, the telia forming separate, deep-seated sori associated with the aecia. Teng (Sinensia 11: 110. 1940) reports similar development for *Xenostele neolitseae* Teng. The peculiar structure of the aecia provides the only distinguishing feature since the teliospores are typically puccinioid. The discovery of species in which the telia do not form within the peridium casts doubt upon the validity of the genus. In the series of obviously closely related species reported here, *P. cinnamomicola* is the only one in which aecia occur; there is no character to indicate clearly that the others should be assigned to *Xenostele*.

*X. neolitseae* is similar to *P. cinnamomicola* but both aecia and telia are considerably wider, as are the teliospores. Tai (Farlowia 3: 135. 1947) has recently described *Puccinia cinnamomi*, on *Cinnamomum* sp. from Szechuan. Aecia are not reported and the teliospores are longer, the lower limit (60  $\mu$ ) corresponding to the upper limit for *P. cinnamomicola*.

While the sorus in the leaf tissue is small the exposed spore pustules may reach a diameter of 1 mm. and frequently coalesce in a single ring 2-3 mm. in diameter.

**Puccinia seposita** Cummins, sp. nov. (fig. 2). Pycniis, aeciis, et urediis ignotis. Teliis hypophyllis, sparsis, brunneis, pulvinatis, maculis brunneis epiphyllis insidentibus, profunde immersis, 75-100  $\mu$  diam.; teliosporis (fig. 2) cylindraceis, utrinque attenuatis, medio non vel vix constrictis, 10-19  $\times$  65-96  $\mu$ ; membrana aureo- vel cinnamomeo-brunnea, 1.5-2  $\mu$  crassa vel ad apicem 3-5  $\mu$ , minuteque rugosa sed apparenter levi, poris germ. in cellulis superioribus apicalibus, in cellulis inferioribus juxta septum dispositis, pedicello tenui, hyalino vel flavido, 3-4  $\mu$  crasso, 150-250  $\mu$  longo, tenuiter tunicato. Statim germ.

On *Benzoin* sp. KWANGSI PROV.: Ling Wang Shan, SAN KIANG HSIEN, Sept. 19, 1933, *Cheo* 2817 (TYPE).

As in other species of this series the exposed spore mass may reach a diameter of 1 mm. The species is clearly distinct from others having deep-seated sori because of the long, narrow spores with uniform side walls. In these characters it is more like *P. lauricola* which, however, has sub-epidermal, broad sori and smooth spores.

**Puccinia morata** Cummins, sp. nov. (fig. 3). Spermagoniis, aeciis, et urediis ignotis. Teliis hypophyllis, sparsis, pulvinatis, castaneo-brunneis, maculis nullis, profunde immersis, 65-80  $\mu$  diam.; teliosporae (fig. 3) cylindraceae, utrinque plus minusve attenuatae, medio non vel vix constrictae, 14-20  $\times$  50-75  $\mu$ ; membrana aureo- vel cinnamomeo-brunnea, minuteque rugosa vel apparenter levi, unilateraliter incrassata, partim tenui 1.5  $\mu$ , partim incrassati 3-5  $\mu$ , ad apicem 6-9  $\mu$  crassa, poris germ. in cellulis superioribus plus minusve subapicalibus, inferioribus juxta septum dispositis; pedicello hyalino, tenui, 3-4  $\mu$  crasso, 100-200  $\mu$  longo, tenuiter tunicato, semipersistenti. Verisimiliter statim germ.

On *Litsea* sp. KWANGSI PROV.: Lao Shan, LING YUIN HSIEN, Apr. 25, 1933, *Cheo* 1950 (TYPE).

This is one of three species exhibiting marked unilateral thickening, the pore-bearing wall always thicker. The apical pore, in these species usually is slightly subapical. Curvature of the spore is much less pronounced than in *P. scimitriformis* which, in addition, has narrower spores. No germinated spores were observed but it is probable that an extended period of rest is not requisite to germination.

**Puccinia scimitriformis** Cummins, sp. nov. (fig. 4). Spermagoniis, aeciis, et urediis ignotis. Teliis hypophyllis, sparsis, castaneo-brunneis, pulvinatis, profunde immersis, 60-90  $\mu$  diam.; teliosporis (fig. 4) plerumque curvatis, cylindraceis, utrinque attenuatis, medio non vel vix constrictis, 12-15  $\times$  60-83 (-90)  $\mu$ ; membrana aureo- vel cinnamomeo-brunnea, minuteque rugulosa vel levi, unilateraliter incrassata, partim tenui 1.5-2  $\mu$ , partim incrassata 2.5-4  $\mu$ ; poris germ. in cellulis superioribus apicalibus, inferioribus juxta septum dispositis; pedicello tenui, hyalino vel flavido, 3-4  $\mu$  crasso, usque ad 150  $\mu$  longo, tenuiter tunicato, fragili. Statim germ.

On *Persea* sp. KWANGSI PROV.: Ta Tseh Shan, YUNG HSIEN, Aug. 23, 1933, *Cheo* 2568 (TYPE).

In this species the unilateral thickening of the side wall is usually pronounced, as is also the associated curvature of the spore. Here the curva-



ture is so conspicuous that the spores are scimiter-shaped. The exposed pulvinate spore mass may reach a diameter of 1 mm.

*Puccinia cara* Cummins, sp. nov. (fig. 5). Spermagonia, aecia, et uredia ignota. Telia hypophylla, sparsa, pulvinata, brunnea, maculis indistinctis vel fere nullis insidentia, profunde immersa, 110–140  $\mu$  diam.; teliosporis (fig. 5) oblongo-ellipsoideis, utrinque rotundatis vel deorsum attenuatis, medio non vel vix constrictis, 14–19  $\times$  47–60  $\mu$ ; membrana pallide castaneo-brunnea, minuteque rugulosa, 1.5–2  $\mu$  crassa, ad apicem 3–5 (–7)  $\mu$  crassa; poris germ. in cellulis superioribus apicalibus, in inferioribus juxta septum dispositis; pedicello hyalino, tenui, 3–4  $\mu$  crasso, 100–200  $\mu$  longo, tenuiter tunicato, fragili. Statim germ.

On *Benzoin* sp. KWANGSI PROV.: Ta Tseh Shan, YUNG HSIEN, Aug. 29, 1933, *Cheo* 2640 (TYPE).

The teliospores of *P. cara* are generally similar in shape to those of *P. machilicola* but average both narrower and shorter. The walls of *P. cara* are thinner and, as shown in the key, the sori are deep-seated and cup-shaped rather than broad and subepidermal.

Occasionally a few abortive spores or pharaphysis-like structures occur in the sori.

*Puccinia aequitatis* Cummins, sp. nov. (fig. 6). Spermagonia, aecia, et uredia ignota. Teliis hypophyllis in greges 3–6 dispositis, pulvinatis, brunneis, profunde immersis, 125–175  $\mu$  diam.; teliosporis (fig. 6) plerumque ellipsoideis, ad apicem rotundatis, deorsum attenuatis, medio leniter constrictis, 17–25  $\times$  45–72  $\mu$ ; membrana aureo- vel pallide castaneo-brunnea, minuteque rugulosa vel apparenter levi, 2  $\mu$  crassa vel ad apicem 3–4  $\mu$ ; poris germ. in cellulis superioribus apicalibus, inferioribus juxta septum dispositis. Pedicello hyalino, tenui, 3–4  $\mu$  crasso, 100–120  $\mu$  longo, tenuiter tunicato, semipersistenti. Statim germ.

On *Benzoin* sp. KWANGSI PROV.: Loh Hoh Tsuen, LING YUIN HSIEN, Apr. 30, 1933, *Cheo* 1995 (TYPE).

*P. aequitatis* is quite similar to *P. cara* but with somewhat larger, especially broader, spores. The wall is more finely rugose than in *P. cara*, with the lower one-half or two-thirds apparently smooth.

#### Explanation of figures 1–8

FIG. 1. Teliospores of *Puccinia cinnamomicola*. From type, *Cheo* 2557. FIG. 2. Teliospores of *Puccinia seposita*. From type, *Cheo* 2817. FIG. 3. Teliospores of *Puccinia morata*; note the unilateral thickening of the walls on the side penetrated by the germ pore and the tendency toward curvature of the spore. From type *Cheo* 1950. FIG. 4. Teliospores of *Puccinia scimitriformis*; curvature of the spore and associated unilaterally thickened side walls are pronounced. From type, *Cheo* 2568. FIG. 5. Teliospores of *Puccinia cara*. The wall in this species is obviously, but minutely rugose. From type, *Cheo* 2640. FIG. 6. Teliospores of *Puccinia aequitatis*; generally similar to *P. cara* but with broader spores becoming smooth on the lower half. From type, *Cheo* 1995. FIG. 7. Teliospores of *Puccinia machili*; this is one of the thick-walled, minutely rugose species showing unilateral wall thickening but without accompanying curvature. The pores obviously penetrate the thick side wall. From type, *Cheo* 1976. Species illustrated in figures 1–7 have deep-seated, cup-shaped telia. FIG. 8. Teliospores of *Puccinia machilicola*; note the obviously roughened wall, the marking consisting of reticulately anastomosing ridges. The sori in this species are broad and merely subepidermal. From type, *Cheo* 330. All figures  $\times$  800.



**Puccinia machili** Cummins, sp. nov. (fig. 7). Spermagoniis, aeciis, et urediis ignotis. Teliis hypophyllis, circinate dispositis vel dense aggregatis, pulvinatis, castaneo-brunneis, maculis brunneis indistinctis vel fere nullis, profunde immersis,  $100-175\ \mu$  diam.; teliosporis (fig. 7) longe ellipsoideis vel cylindraceis, ad apicem plus minusve rotundatis, deorsum plerumque attenuatis, medio non vel vix constrictis,  $17-22 \times (53-) 57-86 (-92)\ \mu$ ; membrana obscure aureo-brunnea vel pallide castaneo-brunnea, minuteque rugosa, unilateraliter incrassata, in parti tenui  $1.5-3\ \mu$  crassa, partim incrassato  $3.5-6\ \mu$  crassa, ad apicem  $6-9\ \mu$  crassa, poris germ. in cellulis superioribus plus minusve subapicalibus, in inferioribus juxta septum dispositis; pedicello hyalino vel flavidulo, tenui,  $3-5\ \mu$  crasso, usque ad  $200\ \mu$  longo, tenuiter tunicato, plus minusve persistenti. Statim germ.

On *Machilus* sp. KWANGSI PROV.: Lao Shan, LING YUIN HSIEN, Apr. 29, 1933, *Cheo* 1976 (TYPE); Apr. 22, 1933, *Cheo*, 1920.

The two collections do not agree in all respects. In the type the sori are confluent in a single circle up to 2 mm. in diameter, the thin side wall of the spore is usually  $3\ \mu$  in thickness, and the spores average slightly broader and shorter than those of No. 1920. The sori in No. 1920 are more tightly grouped, thus not conspicuously circinate, and the thin side walls of the spores are only  $1.5-2\ \mu$ .

The side of the spore on which the pores are located is usually strongly thickened but without the pronounced curvature of the spore that is characteristic of *P. scimitriformis*.

**Puccinia machilicola** Cummins, sp. nov. (fig. 8). Spermagoniis, aeciis, et urediis ignotis. Teliis hypophyllis, brunneis, pulvinatis, sparsis vel in greges usque ad 2 mm. diam. dense aggregatis, subepidermalibus,  $160-200\ \mu$  diam.; teliosporis (fig. 8) oblongo-ellipsoideis vel ellipsoideis vel cylindraceis, medio non vel leniter constrictis, utrinque rotundatis vel deorsum attenuatis,  $16-23 \times (48-) 52-75\ \mu$ ; membrana pallide castaneo-brunnea vel obscure aureo-brunnea, rugoso-reticulata,  $2-3\ \mu$  crassa vel ad apicem usque ad  $5\ \mu$  crassa, poris germ. in cellulis superioribus apicalibus, inferioribus juxta septum dispositis; pedicello hyalino, tenui,  $3\ \mu$  crasso,  $100-200\ \mu$  longo, tenuiter tunicato, fragili. Statim germ.

On *Machilus* sp. KWEICHOW PROV.: SZE NAN HSIEN, Aug. 27, 1931, *Cheo* 330 (TYPE).

This is one of the few species in which the sculpturing of the wall is distinct, although fine. The pattern consists of labyrinthiform ridges, frequently so regularly united as to result in obvious reticulation.

**Puccinia coronopsora** Cummins, sp. nov. (fig. 12). Spermagonia, aecia, et uredia ignota. Teli hypophylla in greges usque ad 3 mm. diam. disposita, pulvinata, castaneo-brunnea, subepidermalia,  $150-300\ \mu$  diam.; teliosporis ellipsoideis, utrinque rotundatis vel deorsum leniter contractis, medio non vel vix constrictis,  $22-26 (-29) \times 43-55 (-60)\ \mu$ ; membrana castaneo-brunnea, minuteque verruculosa,  $3-4\ \mu$  crassa, ad apicem  $5-7\ \mu$  crassa; poris germ. in cellulis superioribus apicalibus inferioribus juxta septum dispositis; pedicello hyalino,  $5-6\ \mu$  crasso,  $75-150\ \mu$  longo, persistenti, prope hilum crasse tunicato, deorsum plus minusve ruguloso.

On *Lindera* sp. KWEICHOW PROV.: Lao Ling, CHIANG K'OU HSIEN, Nov. 16, 1931, *Cheo* 868 (TYPE).

*P. coronopsora* is one of the more distinctive species of the series on



FIG. 9. Teliospores of *Puccinia lauricola*; collections with spores corresponding to these are doubtfully placed in this species. From *Cheo* 409. FIG. 10. Teliospores of *Puccinia lauricola*. From *Cheo* 1890. FIG. 11. Teliospores of *Puccinia lauricola*. This species is typically smooth-spored. From type, *Cheo* 1724. FIG. 12. Teliospores of *Puccinia coronopsora*. From type, *Cheo* 868. Species illustrated in figures 9-12 have broad, subepidermal telia. All figures  $\times 800$ .

Lauraceae because of the dark, ellipsoid spores with thick, uniformly verrucose wall. None of the spores have germinated and it is probable that they require a period of dormancy.

*Puccinia lauricola* Cummins, sp. nov. (figs. 9, 10, 11). Spermagoniis, aeciis, et urediis ignotis. Teliis hypophyllis, sparsis vel 2-3 aggregatis, pulverinatis, castaneo-brunneis, superificialibus, 175-250  $\mu$  diam.; teliosporis cylindraceis, utrinque plus minusve contractis, medio non vel vix constrictis, 13-17 (-19)  $\times$  (52-) 65-96 (-105)  $\mu$ ; membrana obscure aureo-brunnea vel pallide castaneo-brunnea, levi, 1.5-2  $\mu$  crassa, ad apicem 4-12  $\mu$  crassa; poris germ. in cellulis superioribus apicalibus, inferioribus juxta septum dispositis; pedicello hyalino, 4-5  $\mu$  crasso, usque ad 350  $\mu$  longo, persistenti, prope sporum crasse tunicato. Statim germ.

On *Lindera strychnifolia* F. Vill. KWANGSI PROV.: Lao Shan, LING YUIN HSIEN, Mar. 25, 1933, *Cheo* 1724 (TYPE). On *Benzoin* sp. KWEICHOW PROV.: Lao Ling, FAN CHING SHAN, Sept. 7, 1931, *Cheo* 409; KIANGSI PROV.: Poh Luh Tung, SIN Tsz HSIEN, Sept. 28, 1932, *Cheo* 1076. On Lauraceae (indet.). KWANGSI PROV., Lao Shan, LING YUIN HSIEN, Apr. 12, 1933, *Cheo* 1842; Loh Hoh Tsuen, LING YUIN HSIEN, Apr. 16, 1933, *Cheo*, 1890.

It is probable that more than one species is involved in the collections listed here. This is especially true of the two collections on *Benzoin* (Nos. 409 and 1076). The spores (fig. 9) appear to be minutely rugose, whereas they are smooth in the other collections, but the sori are old, parasitized, and in poor condition for study. It should further be noted that they come from different provinces. Probably the two collections do not belong as placed, but better material will be necessary to decide this point.

Of the remaining collections No. 1890 has circinately arranged sori and smooth teliospores (fig. 10) with an apical wall seldom exceeding 5-7  $\mu$  in thickness, while in Nos. 1724 (fig. 11) and 1842 the sori are in tight groups and the apical wall usually 7-12  $\mu$ . The wall is smooth in both. All three of these collections are from the same region. While the teliospores in the latter two collections have not germinated, as have those of No. 1890, it is probable that they are capable of germination without an extended rest period. The pedicels in these three collections are thick-walled, relatively persistent, and appear somewhat gelatinized.

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THE SOUTH AMERICAN SPECIES OF *ARRACACIA*  
(*UMBELLIFERAE*) AND SOME  
RELATED GENERA

LINCOLN CONSTANCE

In our revisionary study of North American Umbelliferae (1944-45), Dr. Mildred E. Mathias and I regarded *Arracacia* Bancroft, with twenty-four species, as the fourth largest genus of the family in the continent, exceeded only by *Lomatium* Raf., with seventy-eight species, *Eryngium* L., with sixty-four, and *Cymopterus* Raf., with thirty-two. The combined ranges of the species of *Arracacia* extend pretty well over the mountainous regions of Mexico and Guatemala, and one reaches Costa Rica and Panama.

For several years, Mr. Ellsworth P. Killip, Curator of the Department of Botany of the United States National Museum, has been urging a study of the South American representatives of this group. In addition to the two properly referred classical species, *Arracacia xanthorrhiza* Bancroft (*A. esculenta* DC.) and *A. moschata* (H.B.K.) DC., in the year 1908 Britton described *A. andina* from Bolivia and Wolff described *A. elata*, *A. incisa*, and *Velaea peruviana* from Weberbauer's Peruvian collections. Finally, Rose attached no less than eight different unpublished names to various herbarium collections. Two of Wolff's species were delineated in the absence of mature fruit, and there has been a good deal of confusion in applying his binomials.

Despite the lapse of forty years since Wolff's and Britton's concern with the genus, the material at hand is still much too meagre to permit anything better than a strictly "pioneer" classification. Many of the collections are immature or lack significant structures; others are not readily referable to any described entity but are scarcely adequate for the typification of a new one, although Wolff would almost certainly have differed with me in this view. I should be surprised if the acquisition of additional material did not necessitate a thorough reappraisal of the admittedly tentative scheme offered below. I think we must recognize, however, the necessity of different "levels" of taxonomic work, and be prepared to construct the best treatment possible with the information at hand. The person interested in floristic considerations will not be helped if the "specialist" refuses to prepare a classification of any group until he has sufficient data at his disposal to make, let us say, statistical analyses and cytogenetical investigations, much as he might wish to employ these tools. The appearance of a provisional treatment should afford a working basis for the taxonomist in need of usable

keys and suitable names for his plants, and at the same time call attention to the utility of further collecting by those in a position to do it.

With considerable misgivings, then, but no apology, the following provisional key is offered to the species of *Arracacia* in South America, with supplementary notes on certain genera which have been in one way or another confused with them.

I am greatly indebted to those in charge of the following herbaria for the opportunity of seeing pertinent specimens: Chicago Natural History Museum (F); Gray Herbarium, Harvard University (GH); Missouri Botanical Garden (MO); New York Botanical Garden (NY); University of California (UC); United States National Museum (US).

*ARRACACIA* Bancroft, Trans. Agr. Hort. Soc. Jamaica **1825**: 3. 1825.

*Arracacha* DC. Bibl. Univ. Sci. & Arts **40**: 78. 1829.

*Velaea* DC. Coll. Mém. **5**: 61. 1829.

*Vellea* D. Dietr.; Steud. Nom. Bot. ed. 2. **2**: 746. 1841.

Stout or slender, erect, herbaceous or somewhat woody, caulescent, branching or simple, glabrous to pubescent perennials, from taproots or tubers. Leaves petiolate, once to several times ternate, pinnate, or ternate-pinnate, the leaflets or ultimate divisions various. Petioles sheathing. Inflorescence of loose to somewhat compact compound umbels; peduncles terminal and lateral, or rarely only terminal, occasionally some umbels sessile. Involucre wanting or vestigial. Involucel of few short to long, narrow bractlets, shorter to longer than the fruit or wanting. Fertile rays few to numerous, spreading-ascending to divaricate and reflexed. Flowers white, greenish-yellow, greenish, reddish-brown or maroon, or purple; petals oblanceolate to obovate with a narrower inflexed apex; calyx teeth obsolete; styles short to long, erect to spreading or reflexed, the stylopodium conic and conspicuous to depressed and indistinct. Carpophore 2-cleft to the base or only bifid at the apex, flat or terete. Fruit lanceolate or oblong to ovoid, usually narrowed at the apex, flattened laterally, glabrous or pubescent; ribs prominent, acute to obtuse, or filiform and indistinct; oil tubes solitary to several in the intervals, 2-several on the commissure; seed subterete in cross section, often channelled under the tubes, the face sulcate or concave.

Type species: *Arracacia xanthorrhiza* Bancroft.

### Artificial Key to the Species

Leaves 1-2-ternate or -pinnate or -ternate-pinnate; leaflets lanceolate to ovate with serrate or dentate and usually incised or lobed margins, and without a prominent callus point; involucre evident; rays and pedicels unwebbed.

Leaflets spinulose-serrate; stylopodium conic; carpophore bifid about  $\frac{1}{2}$  its length; fruit tapering at apex.

Foliage essentially glabrous; flowers greenish-yellow to white; pedicels 4-6 mm. long.

Mericaip ribs obtuse; oil tubes all about the same size.

Fertile rays 4-8; pedicels 4-6 mm. long; mericaip ribs very thick and corky, the intervals broad and shallow; oil tubes large, solitary in the intervals.

1. *A. Pennellii*.

Fertile rays 6-15; pedicels 5-8 mm. long; mericarp ribs thin, the intervals sharply V-shaped; oil tubes very small and indistinct, forming a continous layer between seed and pericarp.

2. *A. elata*.

Mericarp ribs acute; oil tubes of two sizes.

3. *A. Wigginsii*.

Foliage squamulose; flowers usually maroon; pedicels 10-30 mm. long.

4. *A. moschata*.

Leaflets variously serrate to incised or lobed, but not spinulose-serrate; stylopodium depressed; carpophore 2-cleft to the base (unknown in *A. peruviana*); fruit blunt at apex.

Rays 4-8 cm. long; bractlets linear, herbaceous, exceeding the reddish-brown flowers.

5. *A. peruviana*.

Rays 1-4 cm. long; bractlets broad and scarious, or linear and shorter than the purple or greenish flowers.

Bractlets scarious or scarious-margined, lanceolate to obovate.

Bractlets 4-8, obovate to lanceolate, scarious, 5-10 mm. long, exceeding the flowers; mericarp ribs very prominent and corky; oil tubes small, 2-3 in the intervals.

6. *A. incisa*.

Bractlets 3-6, ovate-acuminate, narrowly scarious-margined, 2-6 mm. long, shorter than the flowers; mericarp ribs filiform; oil tubes large, solitary in the intervals.

7. *A. equatorialis*.

Bractlets herbaceous, linear.

Plants 5-12 dm. high; fruit (immature) oblong, 10 mm. long, 2-3 mm. broad, constricted below apex; oil tubes solitary in the intervals.

8. *A. xanthorrhiza*.

Plants 3-4 dm. high; fruit ovoid, 6-7 mm. long, 4-5 mm. broad, not constricted; oil tubes 2-3 in the intervals.

9. *A. andina*.

Leaves ternately decompose, the divisions oblong-linear to filiform with entire margins (in our material) and a prominent callus point; involucre wanting (or vestigial); rays and pedicels webbed.

10. *A. toluensis* var. *multifida*.

# 1. *Arracacia Pennellii* Constance, sp. nov.

Herba crassa suffrutescens caulescens glaucescens glabra, 6-36 dm. alta; folia in ambitu ovato-triangularia, 0.8-2 dm. longa, ternata deinde 1-2-pinnata, foliolis ovato-lanceolatis ovatisve, ad apicem acutis vel acuminatis, ad basin cuneatis rotundatisve, 2-5 cm. longis, 1-2 cm. latis, spinuloso-serratis ad basin lobatis; petioli 1.5-2 dm. longi, ad basin vaginates; folia caulina foliis basilaribus similia, vaginis inflatis; inflorescentia ramosa, pedunculis alternis vel terminalibus, 6-25 cm. longis; involucrelli bracteolae 5-9, lineari-lanceolatae, inaequales, 2-10 mm. longae; radii fertiles 4-8 graciles patenti-adscendentes 3-7 cm. longi; pedicelli fertiles 2-6, 4-5 mm. longi; flores flavido-virides albive, petalis obovatis; stylopodium conicum, stylis gracilibus; carpophorum bifidum, rigidum; fructus ovoideus, 5 mm. longus, 3-4 mm. latus, costis prominentibus obtusis suberosus, pericarpio suberoso, valleculis latibus brevibusque; vittae magnae solitariae in valleculis, 4 in commissuris; semina sub valleculis canaliculata facie sulcata.

Coarse, suffrutescent, branching, caulescent, glaucous herb, 6-36 dm. high, the foliage essentially glabrous; leaves triangular-ovate, 0.8-2 dm. long, ternate-1-2-pinnate, the leaflets ovate-lanceolate to ovate, acute or acuminate, cuneate to rounded at base, the lower distinct and short-petiolulate, the upper sessile and confluent, 2-5 cm. long, 1-2 cm. broad, spinulose-serrate and usually lobed toward the base, the lower surface paler, glabrous, and reticulate, a squamulose tuft on the upper side of the sulcate rachis at the base of the larger leaflets; petioles 1.5-2 dm. long, narrowly sheathing

at base; cauline leaves mostly with wholly sheathing and inflated petioles; inflorescence branching, the peduncles arising terminally and axially 6–25 cm. long, squamulose at apex; involucre of 1–4 sheath-like membranaceous bracts, or wanting; involucl of 5–9 unequal, linear-lanceolate, entire or trifid bractlets 2–10 mm. long, the longer about equaling the flowers but shorter than the fruit; fertile rays 4–8, slender, spreading-ascending, 3–7 cm. long, scaberulous at apex; fertile pedicels 2–6, spreading, 4–5 mm. long, scaberulous; flowers greenish-yellow to white, the petals obovate; stylopodium conic, the styles slender, erect to reflexed; carpophore bifid about  $\frac{1}{2}$ , rigid; fruit ovoid, 5 mm. long, 3–4 mm. broad, tapering at apex, glabrous, the ribs very prominent and corky, obtuse, forming a corky covering over the entire pericarp; oil tubes large, solitary in the very shallow intervals, 4 on the commissure; seed deeply channeled under the intervals, the face sulcate.

TYPE: Moist rocky cañon, alt. 2700–2800 m., Rio San Francisco, above Bogotá, Dept. Cundinamarca, Colombia, 13 September 1917, *F. W. Pennell* 1932 (NY: type).

Specimens examined: COLOMBIA, CUNDINAMARCA: Rio San Francisco, above Bogotá, 13–IX–17, *Pennell* 1932 (NY-type, GH, US); Macizo de Bogotá, Quebrada del Rosal, 3000 m., 29–VI–39, *Cuatrecasas* 5700 (US). NORTE DE SANTANDER: Between Mutiscus and Pamplona, 3400 m., 23–II–27, *Killip & Smith* 19,728 (GH, NY, US). SANTANDER: Cordillera Oriental, páramo de Santurbán, entre Cuesta Boba y el extremo oeste, 3400 m., 27–VII–40, *Cuatrecasas & Barriga* 10,314 (US); Páramo de Romeral, 3800–4100 m., 29,30–I–27, *Killip & Smith* 18,541 (GH, NY, US); vicinity of Vetas, thickets along streams, 3100–3200 m., 16–VI–27, *Killip & Smith* 17,347 (GH, MO, NY, US); Quebrada de Pais, north of La Baja, dense forest, ca. 3200 m., 31–I–27, *Killip & Smith* 18,781 (GH, MO, NY, US).

This species is very similar in general aspect to the next, but its fewer rays, predominantly shorter pedicels, and strikingly dissimilar fruit section, set it well apart. With no collections available to connect the widely separate ranges of the two entities, it seems advisable to regard them as distinct species.

## 2. *ARRACACIA ELATA* Wolff, Bot. Jahrb. 40: 304. 1908.

Stout, clambering, caulescent, branching, up to 4.5 m. high, the foliage essentially glabrous; leaves ovate, 1–3 dm. long, ternate-1–2-pinnate, the leaflets lanceolate to ovate, acute or acuminate, cuneate to rounded at the base, the lower distinct and short-petiolulate, the upper sessile and confluent, 3–6 cm. long, 1–4 cm. broad, sharply spinulose-serrate and often incised toward the base, the lower surface paler and glabrous, strongly reticulate, a squamulose tuft on the upper side of the sulcate rachis at the base of the larger leaflets; petioles 15–45 cm. long, their lower  $\frac{1}{3}$  broadly sheathing; cauline leaves similar, the uppermost with petioles wholly sheathing and inflated; inflorescence branching, the peduncles arising axially, 10–25 cm. long, squamulose at apex; involucre wanting, or occasionally of a single leaf sheath; involucl of 8–10 linear to lanceolate, entire or few-toothed unequal bractlets 3–15 mm. long, the longer exceeding the flowers but shorter than the fruit; fertile rays 6–15, slender, spreading-ascending, 3–6 cm. long; scaberulous at apex; fertile pedicels 3–8, spreading, 5–8 mm. long; flowers greenish, the petals oval; stylopodium conic, the styles slender, recurved; carpophore bifid about  $\frac{1}{2}$  its length, rigid; fruit ovoid, 5 mm. long, 3 mm.

broad, glabrous, the ribs prominent, obtuse, with narrow sharply V-shaped intervals; oil tubes very small and indistinct, forming a continuous layer between seed and pericarp; seed deeply channeled under the intervals, the face sulcate.

TYPE: "Peru: Dep. Amazonas, a Chachapoyos orientem versus; inter Tambo Ventillas et Piscohuañuma, in graminosis, in 3300 m. altitudinis," *Weberbauer 4423*.

Specimens examined: PERU. AMAZONAS: "a Chachapoyos orientem versus; inter Tambo Ventillas et Piscohuañuma," 3000 m., VII-04, *Weberbauer 4423* (type photos: F, GH, UC, US). HUANUCO: Tambo de Vaca, ca. 12,000 feet, 10,24-VI-23, *Macbride 4456* (F, US). AYACUCHO: Choimacota Valley, 3000 m., 28-II, 10-III-26, *Weberbauer 7584* (F, GH, US).

The last collection cited has good, mature fruit, permitting the emendation of Wolff's description, which was based upon immature ones. The close resemblance of this species to the foregoing has been mentioned above.

### 3. *Arracacia Wigginsii* Constance, sp. nov.

Herba crassa suffrutescens caulescens glabra, 2-3 m. alta; folia basalia incognita; folia caulina maiora in ambitu ovato-triangularia, 1-1.5 dm. longa, ternata deinde 1-2-pinnata, foliolis lanceolatis ovato-lanceolatisve, ad apicem acuminatis, ad basin cuneatis rotundatisve, 3-5 cm. longis, 0.8-2 cm. latis, spinuloso-serratis ad basin lobatis; petioli 1-2 dm. longi, ad basin anguste vaginantes; folia caulina superiora similia, petiolo ad laminam vaginato; inflorescentia ramosa, pedunculis terminalibus axillaribusque, 10-16 cm. longis, apice squamuloso; involucelli bracteolae 3-6, lineares oblanceolataeve inaequales, 2-10 cm. longae; radii fertiles 10-15 graciles patenti-adscedentes 3.5-7 cm. longi; pedicelli fertiles 3-8, 4-6 mm. longi; flores flavido-virides albive, petalis obovatis; stylopodium conicum, stylis gracilibus; carpophorum bifidum, rigidum; fructus ovoideus oblongo-ovoideusve, 4-8 mm. longus, 3-3.5 mm. latus, costis acutis prominentibus; vittae vel minimae obscuraeque stratum continuum inter pericarpium et semen formantes vel magnitudine intermediae plerumque solitariae in valleculis omnibus vel aliquis, 2-4 in commissuris; semina sub valleculis canaliculata facie sulcata.

Coarse, suffrutescent, branching, caulescent, 2-3 m. high, the foliage essentially glabrous; basal leaves unknown, the larger cauline leaves triangular-ovate, 1-1.5 dm. long, ternate-1-2-pinnate, the leaflets lanceolate to ovate-lanceolate, acute or acuminate, cuneate to rounded at base, the lower distinct and short-petiolate, the upper sessile and confluent, 3-5 cm. long, 0.8-2 cm. broad, spinulose-serrate and often lobed toward the base, the lower surface paler, glabrous, and reticulate, a squamulose tuft on the upper side of the sulcate rachis at the base of the larger leaflets; petioles 1-2 dm. long, narrowly sheathing below; petioles of the upper cauline leaves wholly sheathing and inflated; inflorescence branching, the peduncles arising terminally and axially, 10-16 cm. long, squamulose at apex; involucre wanting, or of reduced leaf sheaths; involucel of 3-6 unequal, linear to oblanceolate, entire or trifid bractlets 2-10 mm. long, the longer about equaling the flowers but shorter than the fruit; fertile rays 10-15, slender, spreading-ascending, 3.5-7 cm. long, scaberulous; fertile pedicels 3-8, spreading, 4-6 mm. long, scaberulous; flowers "greenish yellow to nearly white," the petals obovate; stylopodium conic, the styles slender, erect to reflexed; carpophore



bifid about  $\frac{1}{2}$  its length, rigid; fruit ovoid to oblong-ovoid, 4–8 mm. long, 3–3.5 mm. broad, the ribs prominent, acute; oil tubes of two sizes: (1) very small and indistinct, forming a continuous layer between seed and pericarp, and (2) vittae of intermediate size, usually solitary in some or each of the intervals, 2–4 on the commissure; seed channeled under the intervals, the face sulcate.

TYPE: Along Pan-American Highway 40 km. south of Cuenca, 10,900 feet, Azuay Prov., Ecuador, 20 September 1944, *Ira L. Wiggins 10,769* (UC 708,757: type).

Specimens examined: ECUADOR. CAÑAR: Vicinity of Cañar, 15-IX-18, *Rose & Rose 22,715* (NY, US). AZUAY: 40 km. south of Cuenca, *Wiggins 10,769* (UC—type); "Mt. Pillshum," 12,000 feet, *Jameson 24* (GH).

The fruits of the *Rose & Rose* collection, although less mature than those of the type, are markedly longer in proportion to their width, but no other significant difference in structure has been detected. This species is very similar to the two foregoing in general aspect and it is, again, the fruit which affords the principal basis for its separation. The peculiar dimorphism of the oil tubes suggests a blend of the kinds of vittae found in *A. Pennellii* and *A. elata*, but scarcely permits these Ecuadorean specimens to be merged with either the Colombian or the Peruvian species.

#### 4. *ARRACACIA MOSCHATA* (H.B.K.) DC. Prodr. 4: 244. 1830.

*Conium moschatum* H.B.K. Nov. Gen. & Sp. 5: 12, pl. 430. 1821.

Stout, clambering, caulescent, branching, up to 1.5 m. high, the foliage squamulose; leaves ovate, 1.5–3 dm. long, bipinnate or ternate-pinnate, the leaflets ovate-oblong to ovate, acute, cuneate or rounded at base, the lower distinct and short-petiolulate, the upper sessile and confluent, 2–5 cm. long, 1–3 cm. broad, sharply spinulose-serrate and incised or pinnatifid, squamulose on the larger veins on the upper surface, the lower surface paler, glabrous and reticulate, a squamulose tuft on the upper side of the sulcate rachis at the base of the larger leaflets; petioles 10–20 cm. long, usually broadly sheathing; cauline leaves with petioles wholly sheathing and inflated; inflorescence branching, the peduncles arising axially, 1.5–3 dm. long, squamulose at apex; involucre of reduced leaf sheaths or wanting; involucre of 3–8 linear to lanceolate, entire or few-toothed bractlets 6–15 mm. long, the longer exceeding the flowers but shorter than the fruit; rays 8–12, stout, spreading-ascending or spreading, 7–13 cm. long, densely scaberulous; fertile pedicels 1–12, spreading, 10–30 mm. long, densely scaberulous; flowers maroon (rarely yellow), the petals oval; stylopodium conic, the styles slender, recurved; carpophore bifid about  $\frac{1}{4}$  its length, rigid; fruit lance-ovoid, 6–8 mm. long, 3–3.5 mm. broad, the ribs very prominent, acute; oil tubes large, usually solitary in the intervals, about 4 on the commissure, sometimes small supplementary ones under the ribs or in the intervals; seed channeled under the intervals, the face sulcate.

TYPE: "crescit in frigidis Provinciae de los Patos, prope Teindala, [Prov. Azuay, Ecuador], alt. 1400 hex.," *Humboldt & Bonpland*.

Specimens examined: ECUADOR. CARCHI: Wooded hills about 5 miles south of Tulcán, 2500 m., 10-VIII-23, *Hitchcock 21,005* (GH, NY, US); between Tulcán and Pun, 3500 m., 11-VIII-35, *Mexia 7580* (US). PICHINCHA: "cult. ad radicem Montes Pichincha, sive Andium Quintensium," III-64, *Jameson* (US—petals yellow); "in Andibus Ecuador-

ensibus," 1857-59, *Spruce 5794* (NY). TUNGURAHUA: "Weg von Paso nach Ambato am Rio Ambato, stelle steinige Überberge, Andem um Ambato, 2850 m., häufig," 6-XI-32, *E. Henrichs 71* (NY).

The long rays and pedicels, the leaf-cutting, and the usually maroon flowers distinguish this species sharply from the preceding. The occurrence of small accessory oil tubes is of interest in the light of the differences in vittae described in the first three species. Jameson's note that this species is "cultivated" may indicate that other species than *A. xanthorrhiza* either are or have been so employed, but I have no further evidence of the domestication of *A. moschata*.

5. *Arracacia peruviana* (Wolff) Constance, comb. nov.

*Velaea peruviana* Wolff, Bot. Jahrb. 40: 303. 1908.

Slender, caulescent, branching, 6-9 dm. high, squamulose to scaberulous throughout, the stem base clothed with dry sheaths, from a branched taproot; leaves ovate-lanceolate, 2-3 dm. long, bipinnate, the leaflets ovate to lanceolate, acute, cuneate at base, the lower distinct and short-petiolulate, the terminal sessile and confluent, 2-5 cm. long, 1-4 cm. broad, coarsely sinuately lobed and mucronulate-serrate, squamulose on the veins and margins, the lower surface paler and reticulate; petioles 1-3 dm. long, sheathing below; cauline leaves pinnate, the uppermost with short, wholly sheathing petioles; inflorescence of alternate axillary peduncles, 7-15 cm. long, squamulose at apex; involucre wanting, or of a single leaf sheath; involucl of 6-10 entire linear bractlets 5-9 mm. long, exceeding the flowers but shorter than the fruit; fertile rays 5-10, slender, spreading-ascending, 4-8 cm. long, squamulose especially at apex; fertile pedicels 2-6, spreading, 5-6 mm. long, squamulose or scaberulous above; flowers reddish-brown, the petals obovate; stylopodium depressed, the styles slender, spreading-erect; carpophore unknown; fruit ovoid, 4-6 mm. long, 3-4 mm. broad, glabrous, the ribs filiform; oil tubes large, solitary in the intervals, 2 on the commissure; seed face deeply and narrowly sulcate.

TYPE: "Peru: Dep. Ancachs, prov. Cajatambo infra Ocos, in 3000-3200 m. alt.," *Weberbauer 2748*.

Specimens examined: PERU. ANCACHS: "prov. Cajatambo infra Ocos," *Weberbauer 2748* (type photo: F). MOQUEGUA: Carumas, 2900 m., 21-II, 6-III-25, *Weberbauer 7269* (F, US). AYACUCHO: Mountains northeast of Huanta, 3200 m., 1,10-II-26, *Weberbauer 7513* (F).

As shown by Coulter and Rose (1900), the type species of *Velaea* DC. (*Ligusticum tolucensis* H.B.K.) is an *Arracacia*, and hence *Velaea* must be merged under *Arracacia*. None of the specimens available for study bear mature fruit, so the description of that organ has been abstracted from Wolff's original description. This species is not likely to be confused with those that precede it, and it is separable from those that follow by its conspicuous linear bractlets and reddish-brown flowers. The Weberbauer collection from Huanta has atypically short involucl, but it may be semisterile.

6. *ARRACACIA INCISA* Wolff, Bot. Jahrb. 40: 305. 1908.

Stout, caulescent, branching, 3-12 dm. high, the foliage squamulose; leaves triangular-ovate to ovate-lanceolate, 1-2.5 dm. long, ternate-pinnate or bipinnate, the leaflets triangular-ovate to ovate-oblong, acute, cuneate or truncate at base, the lower distinct and short-petiolulate, the upper sessile

and the larger pinnately incised, squamulose on the margins and along the veins on both surfaces, the lower surface paler and reticulate, a squamulose tuft on the upper side of the sulcate rachis at the base of the larger leaflets; petioles 8–16 cm. long, narrowly sheathing at the base, the sheaths scaberulous on the veins; cauline leaves with wholly sheathing, inconspicuously inflated petioles; inflorescence branching, the peduncles arising axially and terminally, 2–12 cm. long, squamulose at apex; involucre wanting, or of 1 or 2 sheathing bracts; involucl of 4–8, obovate to lanceolate, scarious, denticulate-margined, unequal bractlets 5–10 mm. long, the green central portion projecting as an acuminate point, exceeding the flowers but shorter than the fruit; fertile rays 4–8, stout, spreading-ascending, 1–4 cm. long, scaberulous at least at apex; fertile pedicels 2–6, stout, spreading, usually 2–5 mm. long, scaberulous; flowers dark purple or greenish, the petals obovate; stylopodium depressed, the styles slender, divaricate; carpophore 2-cleft to the base, lax; fruit ovoid, 5–8 mm. long, 3.5–6 mm. broad, the ribs very prominent and corky, acute; oil tubes small, 2–3 in the intervals, 3–6 on the commissure, some accessory ones frequently under the ribs or in the intervals; seed scarcely channeled under the intervals, the face deeply sulcate.

TYPE: "Peru: in declivibus rupestribus prope Tambo, ad viam ferream inter oppida Lima et Oroya," [Dept. Lima], 2650 m., *Weberbauer 165*.

Specimens examined: PERU. HUANUCO: Steep rocky open grassy slope, ca. 6500 feet, Huacachi, estacion near Muña, 20–V, 1–VI–23, *Macbride 4163* (F, US); in shrub on southwestern canyon slope, ca. 10,000 feet, Yanahuanca, 16,22–VI–22, *Macbride & Featherstone 1244* (F). LIMA: "in declivibus rupestribus prope Tambo, ad viam ferream inter oppida Lima et Oroya," *Weberbauer 165* (type photos: F, GH, UC); Huarochiri, Viso, sandy hillside, sun, 2800 m., 22–IV–39, *Goodspeed, Stork & Horton 11,540* (GH, UC); Prov. Huarochiri, valley of Rio Rimac near Lima—Oroya highway at km. 90 east of Lima, 3000 m., 15,22–III–42, *Goodspeed & Weberbauer 33,059* (GH, UC, US); in firm soil of steep southern slope, sparsely shrubby, ca. 8000 feet, Matucana, 12–IV, 3–V–22, *Macbride & Featherstone 326* (F, US); open slopes, ca. 8000 feet, Matucana, 14,18–III–23), *Macbride 2949* (F, NY, US); rocky slopes, ca. 12,000 feet, Rio Blanco, 8,19–V–22, *Macbride & Featherstone 730* (F, US). CUZCO: Cuzco, 1–IX–14, *Rose & Rose 19,034* (US).

The plants represented by *Macbride 4163* are much larger in stature and fruit than the other collections cited, but these seem to be the only differences. Wolff apparently wrote his original diagnosis from highly unsatisfactory, immature, and possibly sterile material; it is difficult otherwise to reconcile the excellent material now available with his very erroneous depiction of, for example, the involucl and stylopodium. As a consequence, this species and *A. peruviana* have been generally confused by, among others, the writer, although the involucl of the two species are entirely different. The conspicuous scarious involucl setting off the usually deep purple flowers, and the blunt, prominently ribbed fruit make this one of the most distinctive species of the group.

#### 7. *Arracacia equatorialis* Constance, sp. nov.

Herba gracilis ramosa caulescens squamulosa, 4–8 dm. alta; folia in ambitu ovato-triangularia, 6–9 dm. longa, bipinnata, foliolis ovatis, ad apicem acuminatis, ad basin cuneatis truncatisve, 1.5–3 cm. longis, 1–2.5 cm. latis, mucronato-serratis basi lobatis squamulosis; petioli 10–20 cm. longi, ad basin vaginantes; folia caulina similia, foliolis linearibus lanceolatisve elongatis, petiolo ad laminam vaginante; inflorescentia ramosa, pedunculis

verticillatis vel solitariis, ad apicem squamuloso; involucelli bracteolae 3-6, ovato-acuminatae, ad marginem membranaceae, 2-6 mm. longae; radii fertiles 2-6, graciles, patenti-adscendentes, ad apicem scabriusculi, 2-4 cm. longi; flores purpurei, petalis obovatis; stylopodium depressum, stylis gracilibus; carpophorum bipartitum, laxum; fructus ovoideo-oblongus, 8-9 mm. longus, 3-4 mm. latus, costis filiformibus acutis; vittae magnae solitariae in valleculis, 2 in commissuris; semina sub vittis canaliculata facie sulcata.

Slender, erect, caulescent, branching, 4-8 dm. high, the foliage squamulose; leaves triangular-ovate, 6-9 cm. long, biternate or bipinnate, the leaflets ovate, acute or acuminate, cuneate to truncate at base, the lower distinct and short-petiolulate, the upper sessile and confluent, 1.5-3 cm. long, 1-2.5 cm. broad, mucronate-serrate and the larger incised or lobed, squamulose on the sheaths, rachises, veins, and margins beneath with linear scales, squamulose or merely scaberulous above, the lower surface paler and reticulate, a squamulose tuft on the upper side of the sulcate rachis at the base of the larger leaflets; petioles 10-20 cm. long, sheathing only at the base; cauline leaves reduced upwards, with linear to lanceolate, elongate divisions, the obovate petioles wholly sheathing, little inflated; inflorescence branching, the peduncle arising in whorls or singly, 2-12 cm. long, the terminal sometimes subsessile, squamulose at apex; involucre wanting; involucre of 3-6 ovate-acuminate, entire, subequal, narrowly scarious-margined bractlets 2-6 mm. long, shorter than the flowers and fruit; fertile rays 2-6, slender, spreading-ascending, 2-4 cm. long, scaberulous; fertile pedicels 1-3 (-5), stout, ascending, 3-5 mm. long; flowers purple, the petals obovate; stylopodium depressed, the styles slender, spreading-ascending; carpophore 2-cleft to the base, lax, filiform; fruit ovoid-oblong, 8-9 mm. long, 3-4 mm. broad, glabrous, the ribs filiform, acute; oil tubes large, solitary in the intervals, 2 on the commissure; seed channeled under the tubes, the face deeply sulcate.

TYPE: "vicinity of Las Juntas [Prov. Loja], Ecuador," 28 September 1918, *Rose, Pachano & Rose 23,215* (US 1,022,735: type).

Specimens examined: ECUADOR LOJA: Vicinity of Las Juntas, *Rose et al. 23,215* (US—type, GH, NY); entre S. Pedro y Chinchas (unos 55 km. O. Loja), 1600 m., 1-III-47, *R. Espinosa 1305* (UC).

Rose gave to the type collection an herbarium name which is preëmpted in the genus by *A. humilis* Rose, described from Guatemala. The Ecuadorean species is nearest *A. xanthorrhiza* and *A. andina*, differing from the former in its fruit and from the latter in its foliage and oil tubes. The Espinosa collection is immature but probably belongs here.

8. *ARRACACIA XANTHORRHIZA* Bancroft, Trans. Agr. Hort. Soc. Jamaica 1825: 5. 1825.

*Conium Arracacha* Hook. Exot. Fl. pl. 152. 1825.

*Arracacha esculenta* DC. Bibl. Univ. Sci. & Arts 40: 78. 1829.

*Bancroftia xanthorrhiza* Billb. Linn. Samf. Handl. 1: 40. 1833.

Stout, caulescent, branching, 5-12 dm. high, glaucous, the foliage squamulose and scaberulous; leaves broadly ovate, 10-35 cm. long and broad, biternate or bipinnate, the leaflets ovate-lanceolate to triangular-ovate, acuminate, cuneate to rounded at base, the lower distinct and often short-petio-

lulate, the upper sessile and confluent, 4–12 cm. long, 1.5–6.5 cm, broad, coarsely simply or doubly mucronate-serrate and incised or lobed, squamulose or scaberulous on the rachises, veins, and margins with flattened oblong or linear scales, the lower surface pale and reticulate, a squamulose tuft on the upper side of the sulcate rachis at the base of the larger leaflets; petioles 0.8–4.5 dm. long, sheathing only at base; cauline leaves reduced upwards, mostly ternate or 3-parted, with lanceolate, acuminate divisions, the lower alternate and petiolate, the upper often opposite and wholly sheathing with narrow, scarcely inflated sheaths; inflorescence branching, the peduncles arising in whorls or singly, 3–10 cm. long, squamulose or scaberulous at apex; involucre wanting; involucre of 5–8 linear, entire, unequal, herbaceous bractlets 2–5 mm. long, shorter than the flowers and fruit; fertile rays 5–12, slender, spreading-ascending, 1.5–4 cm. long, scaberulous; fertile pedicels 3–8, slender, spreading-ascending, 2–4 mm. long; flowers purple or greenish, the petals oval; stylopodium depressed, the styles slender, ascending; carpophore 2-cleft to the base; immature fruit oblong, 10 mm. long, 2–3 mm. broad, constricted below the apex, glabrous, the ribs prominent, acute; oil tubes rather large, solitary in the intervals, 2 on the commissure; seed channeled under the tubes, the face deeply sulcate.

TYPE: Jamaica, where cultivated from South America, probably Colombia.

Specimens examined: ECUADOR. LOJA: Vicinity of Las Juntas, *Rose et al.* 23,215 *Rose & Rose* (US—foliage). COLOMBIA. ?*Moritz* 1803 (F. NORTE DE SANTANDER: Cordillera Oriental, region del Sarare: Hoya de río Chitagá, á sobre La Cabuya, 1600–1800 m., 13–X–41, *Cuatrecasas, Schultes & Smith* 12,146 (F, GH—foliage). ANTIOQUIA: Cordillera Central, alrededores de Medellín, 1560 m., 1–V–46, *W. H. Hodge* 6861 (GH). CAUCA: Popayan, *Lehmann* B.T.407 (GH—flowers); Cuestá de Tocatá, road from Buenaventura Cali, Western Cordillera, 1500–1900 m., XII–05, *Pittier* 714 (US). PUTUMAYO: Valle de Sibundoy, los alrededores, ca, 2250 m., 18–II–42, *R. E. Schultes* 3267 (GH—foliage). BOLIVIA. LA PAZ: Sorata, IX–I–58, 2697 m., *Mandon* 595 (GH), 22–IV–20, *Holway & Holway* 563 (US—foliage); Sirupaya, 1800 m., 27–XII–06, *Buchtien* 5971 (US—foliage). ECUADOR. TUNGURAHUA: Ambato, 1918, *G. Rose* 38 (GH, US—photo of foliage). PERU. CUZCO: Paruro, Hda. Araypallpa, 3100 m., 28–VII–37, *Vargas* 411 (GH); colinas del Laxaihuamán, 3600 m., XII–28, *Herrera* 858 (F); Ollantaytambo, ca. 3000 m., 24–IV–15, *Cook & Gilbert* 282 (US—foliage); Santa Ana, ca. 900 m., 29–VI–15, *Cook & Gilbert* 1583 (US—foliage); San Miguel, Urubamba Valley, ca. 1800 m., 26–V–15, *Cook & Gilbert* 934 (US—foliage), 935 (US—foliage).

This, the commonly cultivated *arracacha* of northern South America, is represented in herbaria by only unsatisfactory material, and published descriptions are correspondingly inaccurate. I have not seen mature fruit, and it has never been described, to my knowledge; because the plants are ordinarily propagated vegetatively, fruit may not normally ripen. There appears to be no information available on the cultivation of the species that was not incorporated by Hooker (1831) in his description in the Botanical Magazine. None of the material seen is unquestionably from the wild, and I find in it no clues as to the indigenous occurrence and possible original home of the domesticated plant. Hooker's material came from Bogotá, Colombia, by way of Jamaica. What appear to be the most closely related species, however, are *P. equatorialis* of Ecuador and *P. andina* of Bolivia. It is hoped that the publication of this study may stimulate interest in

discovering more information about this crop plant, its domestication, and its origins.

9. *ARRACACIA ANDINA* Britton, Bull. Torrey Club 18: 37. 1908.

Stout, erect, caulescent, branching, 3-4 dm. high, the foliage squamulose; leaves ovate, 1-2.5 dm. long, 1-2-pinnate, the leaflets lanceolate to ovate, usually acuminate and cuneate at base, the lower distinct and short-petiolulate, the upper sessile and confluent, 2-8 cm. long, 1-3 cm. broad, mucronate-serrate and the larger incised or lobed, squamulose on the rachises, veins, and margins with flattened linear scales, the lower surface paler and reticulate, a squamulose tuft on the upper side of the sulcate rachis at the base of the larger leaflets; petioles 15-35 cm. long, sheathing only at base; cauline leaves like the basal, the uppermost with obovate, wholly sheathing, moderately inflated petioles; inflorescence branching, the peduncles arising in whorls or singly, 5-12 cm. long, squamulose at apex; involucre wanting; involucre of 6-8 linear entire unequal herbaceous bractlets 2-5 mm. long, shorter than the flowers and fruit; fertile rays 5-8, slender, spreading-ascending, 2-4 cm. long, scaberulous; fertile pedicels 3-8, spreading, 2-4 mm. long; flowers purple, the petals obovate; stylopodium depressed, the styles slender, spreading; carpophore 2-cleft to the base, the divisions filiform; fruit ovoid, 6-7 mm. long, 4-5 mm. broad, the ribs filiform, acute; oil tubes of intermediate size, 2-3 in the intervals, 4-6 on the commissure; seed shallowly channeled under the larger tubes, the face deeply sulcate.

TYPE: "Ingenio del Oro [Bolivia]," 10,000 feet, III-86, *Rusby 1776* (NY: type).

Specimens examined: BOLIVIA. "Plantae Bolivianae," *Bang 2839* (F, GH, MO, NY, US); Ingenio del Oro, *Rusby 776* (F, NY—TYPE, US).

The broad leaflets, different fruit, and clustered oil tubes separate this species from *A. xanthorrhiza*, and the different involucre and oil tubes distinguish it from *A. equatorialis*, but these appear to be its closest relatives. To either this species or to *A. equatorialis* may belong the three following Peruvian collections which, because of their immaturity or fragmentary nature, I am unable to assign definitely to any species: Huasahuasi, *Ruiz & Pavon* (F); Hacienda Churú, Paucartambo Valley, I-27, *Herrera 1391* (US); San Sebastian, Cuzco, 25-IV-25, *Pennell 13,628* (F). It is possible that there is a Peruvian entity which is distinct from either of these two species, but that decision must await better material.

10. *ARRACACIA TOLUCENSIS* (H.B.K.) Hemsl. var. *MULTIFLORA* (S. Wats.) Math. & Const. Bull. Torrey Club 68: 121. 1941.

Stout, caulescent, branching, 1-3 m. high, the foliage scaberulous, the inflorescence puberulent; leaves deltoid, 2-3.5 dm. long, ternately compound, the ultimate divisions linear-oblong to filiform, acute with a prominent callus point, cuneate at base, sessile, distinct or the terminal confluent, 1-6 cm. long, 0.5-4 (-10) mm. broad, entire (in our material), scaberulous on the veins and margins beneath; petioles 1-4 dm. long, sheathing at base; cauline leaves like the basal, the uppermost usually opposite, greatly reduced and often simple, with obsolete sheaths; inflorescence cymosely branched, of several slender peduncles 3-12 cm. long; involucre wanting; involucre wanting, or vestigial; rays mostly 10-25, slender, spreading-ascending, subequal, 1.5-3 cm. long, slightly webbed at base and often puberu-

lent; pedicels short, spreading-ascending, usually 2-5 mm. long, webbed at base and often puberulent; flowers greenish-yellow; stylopodium conic, the styles short, erect or spreading; carpophore 2-cleft to the base, lax; fruit ovoid-oblong, 6-8 mm. long, 3-4 mm. broad, tapering at apex and base, the ribs prominent, acute; oil tubes large, solitary in the intervals, 2 on the commissure; seed channeled under the tubes, the face deeply sulcate.

TYPE: "on the hills at Rio Hondo," Mexico, *Pringle* 3620.

North American distribution: Hidalgo to Durango, south to Mexico (state) and Oaxaca, Mexico.

South American specimens examined: COLOMBIA. MAGDALENA: Páramos of the Sierra Nevada de Santa Marta, about 30 miles inland from Dibulla, ca. 3850 m., VII-32, *W Seifriz* 432 (US).

The basis for the recognition of this entity in South America is a single fragmentary, badly molded specimen, but there seems to be no question of its identity. Dr. Seifriz's collecting clearly suggests that additional field work in the mountains of Magdalena might prove exceedingly rewarding.

TAUSCHIA Schlecht. *Linnaea* 9: 607. 1834; nomen conservandum. Not *Tauschia* Preissler, 1828.

Two entities from South America have been referred to this genus, which has about twenty species in Mexico and the western United States. The generic lines between *Tauschia* and *Arracacia* have been shifted and redrawn numerous times, and these differences of opinion clearly reveal that there is no sharp morphological break. My recollections of struggling with this problem are still too vivid, however, to make me want to reopen the question now.

1. TAUSCHIA NUDICAULIS Schlecht. *Linnaea* 9: 608. 1834.

To my knowledge, this species, known from Jalisco south to Vera Cruz, Mexico (state), and Puebla, has been reported from South America only on the basis of *Spruce* 6065, "in Andibus Ecuadorensibus." According to Coulter and Rose (1900), "Spruce's specimen from South America is similar to the Mexican specimens in habit, but with a somewhat different fruit section and it may yet prove a distinct species." Judging by the sheet at the Gray Herbarium, the differences, if any, are by no means conspicuous. It may be significant that *Ottoa oenanthoides* H.B.K. has a comparable distribution, being known from Guerrero and Oaxaca, Venezuela, Colombia, and Ecuador.

2. TAUSCHIA JAHNII Rose ex Pittier, *Man. Pl. Usual. Venez.* 299. 1926 (nomen subnudum.).

This name was picked up by Pittier from Rose's annotation of certain Venezuelan collections, of which I have seen the following: "La Puerta, Trujillo, 2000 m.," 16-IX-22, *Jahn* 1136 (US) and "Sierra Nevada de Mérida, 10,000-16,000 feet," XII-23, *de Bellard* 259 (US). Both collections are fragmentary and appear to agree in all respects, including the lack of any mature fruit. While attempting to match these in the Gray Herbarium, I discovered a third and much better sample, but still fruitless, in *Ghiesbreght* 687, "au bord de ruisseaux et des sources d'eau dans les montagnes, Chiapas, etc., Mexico." Steyermark has recently collected the plant twice in Venezuela: "LARA: between Buenos Aires and Páramo de las Rosas,

2285-3290 m.,'' 11-II-44, 55,455 (F) and 55,475 (F), likewise in an immature state. Although all these specimens are superficially reminiscent of *Apium graveolens* L., they are apparently much more closely related to *Arracacia edulis* S. Wats. and *Tauschia nudicaulis* Schlecht., and perhaps constitute an undescribed species in one of these two genera, which would be notable for its leafy stems, small umbels, entire bractlets, and small, blunt fruits (immature).<sup>1</sup>

NEONELSONIA Coult. & Rose, Contr. U. S. Nat. Herb. 3: 306. 1895.

1. NEONELSONIA ACUMINATA (Benth.) Coult. & Rose ex Drude; E. & P. Nat. Pl. 3<sup>s</sup>: 167. 1898.

*Arracacia acuminata* Benth. Pl. Hartw. 187. 1856.

Although this species is commonly confused with *Arracacia Pennellii*, *A. Wigginsii*, and *A. elata* because of a close similarity in vegetative characters, its ellipsoid-cordate, wrinkled fruit and filiform bractlets and pedicels make it readily distinguishable. *Neonelsonia acuminata* is known from Colombia to Ecuador.

2. NEONELSONIA sp.?

To the collection *Pennell 2452*, "Forest, on mount, 2-4 m. s. of Sibate, Cundinamarca, Colombia, 2900-3000 m.,'' 13,15-XII-17 (NY; F, US—photos), Rose gave an herbarium name under *Arracacia*, presumably in recognition of the laxity of the filiform pedicels. The young fruits are broadly ovoid, but too young to be assigned with any certainty to the proper genus. The general similarity of the collection to the preceding species, however, suggests that it may represent an undescribed species of *Neonelsonia*, distinguished from *N. acuminata* by its mucronate rather than spinulose serrations, acute rather than acuminate leaflets, and shorter and broader bractlets.

MYRRHIDENDRON Coult. & Rose, Bot. Gaz. 19: 466. 1894.

As revised by Coulter and Rose (1927), this genus contains four species, one in Guatemala and Costa Rica, the second in Panama, and two others in northern South America. The very large linear or oblong and dorsally flattened fruit is ample to distinguish these plants from any species of *Arracacia*, but vegetative material of the two genera is commonly confused.

1. MYRRHIDENDRON GLAUDESCENS (Benth.) Coult. & Rose, Jour. Wash. Acad. Sci. 17: 214. 1927.

*Arracacia glaucescens* Benth. Pl. Hartw. 187. 1845.

This is presumably the more common of the two species, being known from Colombia to Ecuador. The almost coriaceous leaves with a raised stipular ring at the base of the petiolules and the dissected bractlets distinguish it from any *Arracacia* known to occur in the same area.

2. MYRRHIDENDRON PENNELLII Coult. & Rose, Jour. Wash. Acad. Sci. 17: 214. 1927.

<sup>1</sup> While filing the accumulated Umbelliferae in the Herbarium of the University of California, the writer discovered two more collections of this entity in Steyermark's nos. 48,460 and 49,771 from Guatemala. The second of these has semi-mature fruit, and it is clear from a study of these that all the plants mentioned above under *Tauschia Jahni* Rose are conspecific with *Arracacia vaginata* Coult. & Rose, hitherto known to occur only from Michoacán to Oaxaca, Mexico. Thus *Arracacia vaginata*, with a range extending from Michoacán to Venezuela, constitutes the eleventh species of its genus thus far reported from South America.



Known only from Colombia, this species differs from the preceding in having lanceolate, acuminate, sharply serrate, rather than ovate, obtuse, incised and lobed as well as serrate leaflets, and in having the stipular ring densely hairy.

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## FICUS RETUSA L.

MARY F. BARRETT

For almost one hundred years after their publication *Ficus retusa* L. and *F. nitida* Thunb. were considered separate species. However, the almost identical receptacles and the presence of some intermediate shapes between the most extreme leaf-blades of these small-leaved forms indicated such a close relationship that some botanists came to believe that there was not even a varietal difference between them.

The first statement that *F. nitida* was a synonym of *F. retusa* seems to have come from Benthams.<sup>1</sup> This opinion was held also by most botanists of the rest of the 19th century, especially those who wrote on India and Australia. However, Miquel in 1867 (see below under *Ficus retusa* var. *nitida*) listed *nitida* as "alpha" under *F. retusa*, although this allocation passed almost unnoticed except for Bureau's<sup>2</sup> citation of it as a synonym of *F. retusa*, and Trimen's<sup>3</sup> report of var. *nitida* in Ceylon. Finally King<sup>4</sup> characterized and illustrated *F. retusa* var. *nitida*, but made no reference to Miquel (1867). King has been cited as the author of var. *nitida* by Domin and others.

Most 20th century botanists have accepted *nitida* as a variety. Exceptions who believed it a species were Warburg and others who mentioned it as a cultivated tree in the Americas. It is impossible to judge the opinions of those who have included *nitida* and its synonyms in the whole synonymy of the species *F. retusa*, unless additional text states their views.

King spoke of the "typical *F. retusa*" as contrasted with var. *nitida*, and Koorders & Valeton (see below under *Ficus retusa* var. *typica*) mentioned similar titles; but Domin was the first to publish a valid name for *F. retusa* exclusive of var. *nitida*.

Both varieties have been collected frequently, and var. *nitida* has been widely planted outside its original distribution. Partly for these reasons the species as a whole has acquired an unusually large number of synonyms: some given as new names, and others as incorrect allocations to already existing species. A few synonyms have long been recognized as belonging to one variety or the other, but the rest usually have been listed under the specific name because of the inadequacy of their descriptions, or their inter-

<sup>1</sup> Fl. Hongkongensis 327. 1861.

<sup>2</sup> Ann. Sci. Nat. V. 14: 250. 1872.

<sup>3</sup> Syst. Cat. Pl. Ceylon 84. 1885.

<sup>4</sup> Ann. Bot. Gard. Calcutta 1: 51. pl. 62. 1887-1888.

mediate status between vars. *typica* and *nitida*, or in the belief that the two forms are synonymous.

Since *F. retusa* is an important, although confused and debatable East Indian species, and since var. *nitida* is quite separable from the typical variety by habit as well as leaves it has seemed well to differentiate the synonyms of each form, incidentally eliminating numerous homonyms which have been associated with them. Var. *nitida*, as the more distinctive, will be treated first. In selecting its synonyms the principal characters used are the short, blunt, acuminate apex and the narrowed base of the leaf, as well as its shining upper surface; and the banyan habit. Synonyms which show an insufficient number of these characters, or which do not point towards var. *nitida* by their own synonymy or by the opinions of authorities are relegated for the present to var. *typica*.

The description and distribution of var. *nitida* have been made up from living trees observed at numerous places in Florida, and from herbarium specimens and texts seen mostly at the New York Botanical Garden. Var. *typica* was studied only through herbarium specimens and texts.

The following specimens furnish good examples of the leaves, and sometimes of the receptacles, of var. *nitida*: *F. nitida* from the Botanic Garden of Calcutta, a part of no. 4523 D in Wallich's catalog; *Urostigma nitidum*, Kollmann 1838, Hongkong; and *F. retusa*, R. C. Ching 5185, Kwangsi Province, China. Good examples of var. *typica* are: *F. retusa*, L. J. Brass 3592, Papua; *Urostigma nitidum*, W. C. 2651, Campbell 82, Peninsular India (from the Wight herbarium); *F. retusa*, A. W. Herre 378, Celebes; and *F. retusa*, W. J. Lutjeharms 4212, S. Sumatra.

Illustrations of leaves, receptacles, and flowers of both varieties may be seen in King's text (1887-1888; 1: pls. 61, 62, 84). Leaves of var. *typica* are shown in *Hawaiian Forester and Agriculturalist* 6: pl. 125. 1909. Pl. 732 in the *Atlas* of Koorders & Valetton (1916) bears leaves and receptacles of var. *nitida*, although some leaves are labeled merely *F. retusa*. Mowry<sup>5</sup> pictures var. *nitida* under the name *F. retusa* (*F. nitida* Thunb.). Sata<sup>6</sup> illustrates var. *typica*.

*FICUS RETUSA* var. *NITIDA* (Thunb.) Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 288. 1867. *Itti-arealou* Rheede, Hort. Mal. 3: 69. pl. 55. 1682.

*Ficus malabarica*, folio mali cotonei, fructu exiguo, sanguineo, plano-rotundo J. Comm. in Rheede, Ibid. 3: 70. 1682.

Garden mangrove Hughes, Nat. Hist. Barbadoes 193. 1750.

*F. microcarpa* L.f. Suppl. Pl. 442. 1781. Not of Vahl, Blume 1825, or F. Villar.

*F. nitida* Thunb. Diss. Fic. 5, 10-11, 15. 1786. Not of Heyne Hb. ex Roth, or Hook. 1825.

*F. bentamina* Thunb. Ibid. 11. 1786. Not of L.

? *F. retusa* Lam. Enc. 2: 496. 1788. Not of L.

<sup>5</sup> Fla. Agr. Extens. Bull. 95: f. 42. Ap. 1938.

<sup>6</sup> Contr. Inst. Hort. & Econ. Bot. Taihoku Univ. 32: pls. 18, 19. 1944.

- F. pertusa* Willd. Sp. Pl. 4: 1144. 1806. Not of L. f., Bory, or of some writers on W. I. and Mexico.  
*F. rubra* Roth in Roem. & Schult. Syst. Veg. 1: 507. 1817. Not of Vahl or Blume.  
*F. indica* Heyne Hb. ex Roth, Nov. Pl. Sp. 391, as syn. 1821. Not of L. or Miquel.  
*F. arbutifolia* Link, Enum. 2: 450. 1822.  
*F. condaravia* Hamilt. Trans. Linn. Soc. 15: 131. 1827.  
*F. reflexa* Hamilt. Hb.; Wall. Cat. no. 4523 F. 1831. Not of Thunberg.  
*F. pallida* Wall. Cat. no. 4567. 1831. Not of Vahl or Grisebach.  
*F. pallescens* Steud. Nom. Bot. ed. 2. 1: 637. 1840.  
*F. nitida*  $\beta$  *reflexa* Steud. Ibid.  
*Urostigma nitidum* Gasp. Nov. Gen. Fic. 7. 1844. *Nomen nudum*.  
*U. amblyphyllum* Miq. Hook. Lond. Jour. Bot. 6: 569. 1847.  
*U. pisiferum* Miq. Ibid. 6: 580. 1847.  
*F. pisifera* Hook. Hb. ex Miq. Ibid., as syn. Not of Wallich.  
*U. nitidum* Miq. Ibid. 6: 582. 1847.  
*F. elliptica* Hook. Hb. ex Miq. Ibid., as syn. Not of H. B. K., Miquel 1848, or Grisebach 1860.  
*U. microcarpum* Miq. Ibid. 6: 583. 1847.  
*U. arbutifolium* Miq. Versl. Med. Kon. Akad. Amsterdam 13: 412. 1862.  
*F. prolixa* Vieill. & Depl. Ess. Nouv. Calédonie 114. 1863. Not of Forster f.  
*F. amblyphylla* Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 286. 1867.  
*F. retusa*  $\alpha$  *nitida* Miq. Ibid. 3: 288. 1867.  
*F. retusa*  $\gamma$  *pisifera* Miq. Ibid. 3: 288. 1867.  
*F. rubra* var. *amblyphylla* Baker, Fl. Mauritius 285. 1877.  
*F. sp.* Combs, Trans. St. Louis Acad. Sci. 7: 465. 1897.  
*F. bengolensis* Schimp. Pfl. Geog. ed. 1. pl. 162. 1898. Not of L.

Glabrous shrub or tree to 25 or 30 m. in native home; banyan type, with secondary trunks originating from aerial roots starting from the first stem and the largest branches and fastening themselves in the ground; young trunks light-colored, unfurrowed, branching near ground, developing prop roots and buttresses; crown very spreading; branches sometimes striate or angular; twigs slightly 3-angled, tan-colored with light-colored lenticels; terminal buds conical-subulate, green, about 2 cm. long; leaves evergreen; petioles mostly about 5–10 mm. long, slender, grooved, lighter green than blades when fresh, darker when dry; blades laurel-like, typically obovate, but also elliptic or ovate; many about  $7.5 \times 3.5$  cm., but to  $12.5 \times 5.5$  cm.; apex slightly narrowed and then rather abruptly short-blunt-acuminate; base tapering to petiole; margin entire, cartilaginous; upper surface dark green, waxy, shining; under surface paler, dull; texture thin-leathery; veining distinct beneath when dry; midrib continuous; one pair of basal veins not much thicker than the lateral veins, parallel to the margin and reaching almost the middle of the blade; 4–7 sets of slender, almost parallel lateral veins, leaving the midrib at an upper angle of  $40\text{--}50^\circ$  and uniting in indentations with the submarginal vein; several forked thinner veins in each intervein, parallel to the lateral, reaching the submarginal vein at slight indentations; reticulum faint; receptacles axillary, paired but sometimes appearing crowded, on new wood, depressed-globose, 5–6 or rarely to 8 mm. in diameter, glabrous; apex slightly raised at first, ostiole closed by 3 close triangular bracts; base rounded, becoming red, purple, or blackish, sessile in a flat inconspicuous cup made by 3 ovate basal bracts; flowers (according to Gagnepain) of all three kinds in one receptacle, short-pedicelled, 3–4 sepals;

sepals of male flowers obovate, spatulate, about one mm. long, very obtuse; stamen one, anther short-mucronate; sepals of female flowers ovate, obtuse, 1-2 mm. long; ovary oblong, then pyriform, 2 mm. long; style lateral, filiform, dilated and slightly papillose at summit; (gall flowers not mentioned).

TYPE: none cited by Thunberg. (See comment on *F. nitida* Thunb., below).

Distribution: northeastern India and some states to the north, Burma, Indo-China, Malaya, South China, Formosa, Philippines, Caroline Islands, Australia, New Caledonia.

Common Names: laurel fig, shining fig-tree; Spanish, Cuban, and Indian laurel; small-leaved, bastard and Chinese banyan. From the prevalence of this variety Fuchow (South China) has been called the Banyan City.

Economic Importance: the ease with which var. *nitida* can be propagated by cuttings from its aerial roots may be responsible for its wide distribution as a cultivated tree. When it is used along streets its aerial roots must be cut off to keep the tree within bounds.

*FICUS RETUSA* var. *TYPICA* Domin, Bibl. Bot. 89: 563. 1921.

*F. retusa* L. Mant. 129. 1767.

*Perula retusa* Raf. Sylv. Tell. 58. 1838.

*Urostigma retusam* Gasp. Nov. Gen. Fic. 7, 1844. *Nomen nudum*.

*U. retusum* Miq. Hook. Lond. Jour. Bot. 6: 581. 1847.

*U. ovoideum* Miq. Ibid. 6: 581. 1847.

† *U. accedens* β *latifolia* Miq. Fl. Ind. 12: 347. 1859.

*F. dilatata* Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 218. 1867.

*F. retusa* β *ovoidea* Miq. Ibid. 3: 288. 1867.

*F. retusa genuina* King ex Koord. & Val. Booms. Java 11: 38. 1906.

*F. retusa* forma *typica* King ex Koord. & Val. Ibid. 11: 133. 1906.

*F. retusiformis* Lévl. Fedde, Repert. 8: 549. 1910.

*F. retusa* var. *retusa* Haines, Bot. Bihar & Orissa 829. 1924.

(It will be noticed that some of the above synonyms are incorrect in form. They are cited to show that several attempts were made to form a variety correlative with *nitida*.)

In comparison with var. *nitida* the typical form of *F. retusa* has at the most only a few air roots, and usually none which forms a secondary trunk. The dull-surfaced leaves commonly are rather broad-ovate or broad-elliptic instead of obovate, and have an obtuse, apicular, or barely elongated apex and a rounded or very slightly narrowed base. The receptacles may reach 10 or even 13 mm. in diameter. Their basal bracts seem to be larger and more spreading than those of var. *nitida*, and tend to remain on the twig after their receptacles have fallen off. The female flowers are described by King as almost or quite sessile. The gall flowers, according to Sata (1944; pt. 1: 23), have a globose ovary, a short style, and a cylindric or clavate stigma.

TYPE: India.

Distribution: Peninsular India; also about the same distribution as var. *nitida*, except for Java, according to reports and specimens.

Common Names: Blunt-leaved fig, retuse fig.

Economic Importance: latex furnishes some rubber, bark said to be used in paper-making, tree cultivated as decoration for lawns and streets.

EVALUATION OF SYNONYMS OF VAR. *NITIDA*

*Itti-arealou* Rheede. The first published mention of a tree known to belong to *F. retusa* is believed to be the description, accompanied by a plate, of *Itti-arealou*. The text is so occupied by an account of its banyan habit, most of it taken from the description by Clusius of *F. indica* (*F. bengalensis* L.), that it dismisses the leaves with the remark that they are similar to, but smaller than those of *Itti-alou*, (a tree often confused with *F. retusa*, but usually believed to be the prototype of *F. benjamina* L.) Rheede's plate of *Itti-arealou* pictures leaves of the *typica* form, but with longitudinal parallel veins. Since such veining almost never is seen in *Ficus* the assumption is that the artist was told to depict parallel veins, but was not shown the direction in which they should run. The receptacles are represented satisfactorily in both text and plate. In spite of the leaf-form and the location of the tree in the southwestern part of India this reference, which Thunberg cited for *F. nitida*, has been almost universally accepted because of the banyan habit, which Rheede further emphasized by citing vernacular names meaning "Little Root-Tree".

Commelin's polynomial. At the end of Rheede's text the editor, J. Commelin, furnished a descriptive name for *Itti-arealou*, in which the characterization of the leaf as quince-like was drawn from Clusius and was inaccurate as to both shape and surface.

Garden Mangrove. Less than 70 years after the publication of *Itti-arealou* Hughes declared that the Garden Mangrove of Barbados was a kind of fig-tree which could be propagated by its aerial roots. This has been identified by Maycock<sup>7</sup> as "*F. nitida*." Hughes' probably was almost the first of many reports of this variety in the West Indies.

Synonyms from Thunberg. Thunberg's description of *F. nitida* added little except the word *shining* to Rheede's text. In fact, his characterizations of the leaves and receptacles were merely those of Rheede's plate, translated into words. Thus he omitted the distinguishing characters of leaf-shape and banyan habit. However, Willdenow<sup>8</sup> reported the leaves as obovate, very short-obtusely acuminate, dark green above, and 5 cm. long. Vahl<sup>9</sup> called them acuminate at each end.

Although Thunberg listed no location of his type of *F. nitida*, merely implying that it came from Malabar, he may have intended Rheede's species simply as a reference. According to Aiton<sup>10</sup> specimens of *F. nitida* were introduced into Kew Gardens in 1786 (the year of Thunberg's publication) from the East Indies by Sir Joseph Banks. There is a possibility that these specimens came from one of the large East Indian islands touched by Banks, perhaps Java, where, according to Koorders & Valetton (1906; 11: 114-116) the typical Himalayan form of *F. retusa* L. breaks up and encroaches on var. *nitida*, and the latter is very common. Thunberg may have come across *F. nitida* from that source: a more likely one than the southwestern coast of India proper. In that case the question is: how did

<sup>7</sup> Fl. Barbadosensis 406. 1830.

<sup>8</sup> Sp. Pl. 4: 1145-1146. 1806.

<sup>9</sup> Enum. Pl. 2: 191. 1806.

<sup>10</sup> Hort. Kewensis ed. 2. 5: 488. 1813.

var. *nitida* get to Malabar, if *Itti-arealou* really is Thunberg's species? One answer is that it may have been imported because it was an interesting and easily propagated tree, just as it came so early to the West Indies that it was reported by Hughes in 1750 as a 40-ft. tree whose cultivation already was understood.

A more valuable contribution to var. *nitida* from Thunberg was his description of what he thought was *F. benjamina* L. This seems to have been based upon a specimen from a Javan tree which Thunberg later sent to van Royen. Although Thunberg referred to Linnaeus he listed few characters given by that author, but repeated some of his own which he had stated for *F. nitida*. *F. microcarpa* L.f. was cited as a synonym.

The Thunberg specimen of "*F. Beniamina*", which later came into Blume's possession, was declared by Blume (below) to be *F. microcarpa*, and this, as will be shown, is var. *nitida*. Miquel (1867) cited *F. benjamina* of Thunberg as a synonym of var. *nitida*, and King (1887-1888; 1: 180) has said that it probably belongs there. Other authors whose reports of *F. benjamina* should be allocated to var. *nitida* are Willdenow (1806; 4: 1143), Willdenow,<sup>11</sup> Persoon,<sup>12</sup> and Kunth,<sup>13,14</sup> Roxburgh<sup>15,16</sup> usually is included in this list because of the suggestion of Wight<sup>17</sup> that Roxburgh's description in 1832 of *F. benjamina* Willd. might be of *F. nitida*. Although pl. 657 in Wight's book, labeled *F. nitida* and supposed to represent Roxburgh's tree, resembles var. *typica* in leaf-shape, as does the specimen *Urostigma nitidum* from Wight's herbarium (already mentioned), Wight's text says that *F. nitida* has secondary trunks. Cooke<sup>18</sup> has said that *F. benjamina* Graham<sup>19</sup> is *F. retusa*. Since Cooke included *F. nitida* as a synonym of *F. retusa*, and since Graham mentioned shining polished leaves, the latter's *F. benjamina* probably belongs to var. *nitida*.

*F. retusa* Lamarck. The inclusion of this name as a synonym rests upon very slight evidence; that is, that the branch seen by Lamarck came from Java (where *nitida* and not *typica* is the usual variety). It would be impossible to cite all the references which have called var. *nitida* by the name of *F. retusa*.

*F. microcarpa*. Between the dates of publication of *F. retusa* and *F. nitida* the younger Linnaeus described *F. microcarpa* from Java. This was cited as a synonym of *F. benjamina* by Willdenow (1806) and others, as well as by Thunberg, although Willdenow (1809; suppl. 69) listed it as a species without description. In 1810 J. E. Smith<sup>20</sup> cited it as a synonym of *F. nitida*.

The reference which did most toward allocating *F. microcarpa* L. f. to

<sup>11</sup> Enum. Hort. Berolinensis 1063. 1809.

<sup>12</sup> Syn. Pl. 2: 610. 1807.

<sup>13</sup> Ind. Sem. Hort. Berol. 1846: 20. 1846.

<sup>14</sup> Ann. Sci. Nat. III. 7: 250. 1847.

<sup>15</sup> Hort. Bengalensis 103. 1814.

<sup>16</sup> Fl. Ind. ed. 2. 3: 550. 1832.

<sup>17</sup> Ic. Pl. Ind. 2: (4) 1. 1843.

<sup>18</sup> Fl. Pres. Bombay 2: 647. 1907.

<sup>19</sup> Cat. Pl. Bombay 191. 1839.

<sup>20</sup> Rees, Cycl. 14: Ficus no. 50. 1810.

var. *nitida*, and toward filling in at an early date the distinguishing characters of that variety was the work of Blume,<sup>21</sup> in 1836. Blume<sup>22</sup> already had described as *F. microcarpa* a climbing vine, now believed to be *F. ramentacea* Roxb., but to this he did not refer in 1836. He based the later material upon a very old Javan tree which he thought was made up by the intertwining of *F. microcarpa* and *F. benjamina* L. He said that Thunberg had not differentiated the two species, but had called the composite plant *F. benjamina*; and that the specimen sent by him to van Royen was *F. microcarpa*, which (Blume said) had been commonly confused also with *F. nitida* and sometimes with the (South) American species *F. pertusa* L.f.

Although Blume thus rather hesitatingly differentiated *F. microcarpa* from *F. nitida* his description of the former, his comparisons of it with *F. benjamina* and other species, and his reference to *Itti-arealou* Rheede as a synonym served to direct *F. microcarpa* toward var. *nitida*. Miquel (1867) cited it as a synonym of *F. retusa* a *nitida*, and other botanists have accepted it as belonging to the species *F. retusa*. Its specific name would supplant *nitida* if the latter were considered a species.

*F. pertusa*. Under this name a shrub from Surinam (Dutch Guiana) was described briefly by Linnaeus f.<sup>23</sup> in almost the same terms that applied also to var. *nitida*, except for smaller and peduncled receptacles. The individuality of this species is shown in a plate of Plumier's,<sup>24</sup> cited by the younger Linnaeus as a reference, which agrees well enough with two specimens of *F. pertusa*: Otto Kuntze Hb. from "Mattagrosso" (Matto grosso, Brazil?), and W. E. Broadway 8169 in a collection from the Royal Botanic Gardens, Trinidad and Tobago, W. I. These show elliptic rather than obovate leaves, with many more lateral veins than in var. *nitida*. Both the plate and the second specimen have peduncled receptacles.

In spite of these differences *F. nitida* commonly was called *F. pertusa* in herbaria of the West Indies, according to Warburg<sup>25</sup>. He also asserted that *F. sp.* Combs, and *F. pertusa* of Willdenow (1806) and of A. Richard<sup>26</sup> were *F. nitida*. Similar synonyms, listed by Maycock (1830; 407), were *F. pertusa* of Aiton (1813; 5: 487) and of Sprengel.<sup>27</sup> To them probably should be added reports of *F. pertusa* by Willdenow,<sup>11</sup> Roth (1821; 288), Link (2: 449), and Kunth<sup>13</sup> and (1847; 249-250). But the earlier text on *F. pertusa* by Aiton<sup>28</sup> bears evidence that it refers to the species of Linnaeus f.

*F. rubra*. The source usually given for *F. rubra* Roth is Roth's *Novae plantarum species* 391. 1821. But this name had been published previously by Roemer & Schultes, who referred to Roth's manuscript. *F. rubra*, without the references cited by Roth, and with the omission of his variety *acuminata*, was allocated to var. *nitida* by Miquel (1867). King (1887-1888; 1: 179) also has stated that *F. rubra* Roth belongs to that variety.

<sup>21</sup> Rumphia 2: 17-21. 1836.

<sup>22</sup> Bijdr. 442. 1825.

<sup>23</sup> Suppl. Pl. 442. 1781.

<sup>24</sup> Pl. Amer. pl. 132 f. 2. 1755.

<sup>25</sup> Urban, Sym. Antillanae 3: 489. 1903.

<sup>26</sup> Sagra, Hist. Cuba 11: 221. 1850.

<sup>27</sup> Syst. Veg. 3: 781. 1826.

<sup>28</sup> Hort. Kewensis ed. 1. 3: 452. 1797.



*F. indica*. Roth based *F. rubra* upon an East Indian herbarium specimen which Heyne had called *F. indica*. The original *F. indica* was the name which Theophrastus gave to the huge banyans seen in the Indian Punjab by the army of Alexander the Great. The references cited by Linnaeus show that his *F. indica* in *Species plantarum* is the same species. However, Linnaeus, who apparently never had seen *F. indica*, unwittingly gave the title *F. benghalensis* (*F. bengalensis* is incorrect spelling) to a plant of the same species, which he had studied in Leiden, and which had been described and illustrated under different names by other botanists. In time it was realized by later writers that *F. indica* and *F. bengalensis* were the same, and the latter name was perpetuated, partly because of its better descriptions and references, but principally because *F. indica* L. had been given a variety,  $\beta$ , by Linnaeus, which was a conglomeration of several American species, mostly from the West Indies, of a tree from Amboina, and of *Tsiela* Rheede, a species now usually known as *F. tsiela* Roxb., but more correctly entitled *F. amplissima* J. E. Smith.

*F. indica* had almost disappeared from taxonomy when Miquel (1867; 3: 263, 287) revived it as the title of a Philippine specimen which he previously had called *Urostigma tjiela* and had assumed was a narrow-leaved form of *Tsiela* Rheede. This slight and erroneous connection with one of the Linnean synonyms of a name which very properly had been discontinued seems to have been Miquel's only reason for the use of the term *indica*. In apparent violation of the rules of botanical nomenclature *F. indica* as a title has been employed by such authorities as King, Merrill, and others.

This explanation is made necessary by the appearance now and then of herbarium specimens named *F. indica* which resemble one or the other varieties of *F. retusa* rather than the Philippine *F. indica* of Miquel. Certain references in literature also suggest an occasional misnomer.

*F. arbutifolia*. Warburg<sup>29</sup> and Britton & Wilson<sup>30</sup> have cited *F. arbutifolia* Link as a synonym of *F. nitida*. Link's description was brief but suggestive of var. *nitida*. A detailed characterization by Kunth (1846; 19. 1847; 249) was complicated with a large number of horticultural and questioned synonyms, which seem unimportant or incorrect. No distribution was reported by Link, Kunth, or Miquel (who increased the synonymy). Warburg's Berlin connections probably caused him to recognize this species as the *F. nitida* which he had seen in the West Indies and elsewhere.

*F. condaravia*. This species was said by Hamilton to be the same as *Itti-arealou* Rheede and *F. nitida* Thunb., and its description bears out that allocation. King (1887-1888; 1: 180) declared that *F. condaravia* appeared to be *F. retusa*, but did not specify the variety.

*F. reflexa*. This specimen from Hamilton's herbarium was placed by Wallich, with a question mark, under *F. nitida*. Steudel considered it a variety of that species and suggested a comparison with *F. condaravia*. King (1887-1888; 1: 50) cited *F. reflexa* and the other sections of Wallich's no. 4523 as synonyms of *F. retusa*.

<sup>29</sup> Urban, Symb. Antillanae 4: 198. 1905.

<sup>30</sup> Sci. Surv. P. Rico 52: 239. 1924.

*F. pallida* Wall. has been accepted for *F. retusa* by King. As the specific name had been published for a different *Ficus* by Vahl, Steudel changed Wallich's title to *F. pallescens*. Thwaites<sup>31</sup> allocated *F. pallida* Wall. with *F. nitida* Thunb. and *F. retusa* L. to *Urostigma retusum*, and Miquel (1867) accepted it as a synonym of *F. retusa*  $\gamma$  *pisifera* on Thwaites' authority.

Species of *Urostigma* and their later allocations. Gasparrini in 1844 and later<sup>32</sup> listed "*retusam*" (*retusum*) and *nitidum* under his new species *Urostigma*; but failed to mention the original authors. Therefore the credit for these names passed to Miquel (1847), who was responsible also for other species of *Urostigma* related to *F. retusa*. Benth<sup>1</sup> cited most of them as synonyms of *F. retusa*, and Miquel (1867) listed them as distinct species or as varieties of *F. retusa*.

*U. amblyphyllum* was described from an East Indian specimen in Hooker's herbarium which was labeled *F. nitida*. In spite of the blades' obtuse or slightly retuse apex and its obtuse or slightly emarginate base King (1887-1888; 1: 179) asserted that *U. amblyphyllum* and *F. amblyphylla* were synonyms of *F. rubra* Roth which, he said, equalled *F. retusa* var. *nitida*. Baker previously had allocated *U. amblyphyllum* to *F. rubra* as a variety.

The basis of *U. pisiferum* was *F. pisifera* Hb. Hook., although *F. condaravia*, omitting synonym *Itti-arealou*, also was cited. Miquel eventually called this form *F. retusa*  $\gamma$  *pisifera* without further description, but his original characterization and Hamilton's synonym suggest that it belongs to var. *nitida*. A synonym added to it in 1867 is *F. pallida* Wall., which would carry with it *F. pallescens* Steud. (see above). *U. pisiferum* is acknowledged as *F. retusa* by many authorities.

Miquel's treatment of *U. nitidum* in 1847 included synonyms and references mentioned by others, and also two specimens from Hooker's herbarium, labeled *F. nitida* and *F. elliptica*. The latter is not to be confused with a parasitic vine from the Philippines, to which Miquel<sup>33</sup> later gave the name *F. elliptica*. Somewhat the same material was repeated by Miquel in 1859; but in 1867 the form was considered by him a variety of *F. retusa*.

The discussion of *U. microcarpum* by Miquel (1847) and later (1859; 12: 346) was mainly a summary of that of Blume (1836) for *F. microcarpa* L.f. (above). Two synonyms cited by Miquel apparently do not apply to var. *nitida*, of which *F. microcarpa* is a synonym. These are *F. littoralis* Blume which Blume suggested as a variety of *F. microcarpa*, but which seems unlike the species *F. retusa*; and *F. leptocarpa* Steud., which Miquel himself removed in 1867 when he transferred the *microcarpa* forms to *F. retusa*  $\alpha$  *nitida*. *F. leptocarpa* probably is *F. ramentacea* Roxb. *F. littoralis* possibly is var. *typica*.

*U. arbutifolium* was returned to *F. arbutifolia* Link by Miquel (1867; 3: 298). This reference contained only Kunth's suggestions as to synonyms of *F. arbutifolia* (see above), with one omission; and included one horticultural and one herbarium synonym of Miquel's own.

*F. proluxa* at first was thought to be the species to which Forster f. had

<sup>31</sup> Enum. Pl. Zeylandiae 265. 1864.

<sup>32</sup> Rendic. Acad. Napoli 4: 398. 1845.

<sup>33</sup> Fl. Ind. Batavae 12: 345. 1859.

given that name; but later was identified by Bureau<sup>2</sup> as *F. retusa* var. *nitida*. Specimens had been found in New Caledonia.

*F. sp.* Combs. A collection note reported this only as a large tree in Cuba, perhaps cultivated. It was allocated to *F. nitida* by Warburg.<sup>25</sup>

*F. bengalensis* Schimp. The mislabeling of this picture of a banyan was corrected to *F. retusa* var. *nitida* by Koorders & Valeton (1906; 11: 112, 114) and a plate labeled *F. retusa* was substituted for it in the Faber edition of *Pflanzengeographie* 1: pl. 128. 1935.

#### EVALUATION OF SYNONYMS OF VAR. *TYPICA*

*F. retusa* L. The original Linnean description of *F. retusa* contains the leaf-character cuneiform-obovate, which is more typical of var. *nitida* than of var. *typica*. But because it also speaks of the leaves as *oblong*, a term sometimes used by early botanists to denote *elliptical*, and of their apex as very obtuse this text has been thought to apply to var. *typica*. Specimen *T.M. Tsui* 373 from Kwangtung, China has a cuneiform-obovate leaf-shape and an almost perfectly obtuse apex. It is labeled *F. retusa* and evidently is var. *typica*. *Retuse* now means notched when applied to leaves and seems inappropriate here, although very rarely it has been stated as one of their characters. Thunberg's description of *F. nitida* calls the receptacles retuse-umbilicate, probably referring to their eventually depressed apex. Lévillé says that *F. retusifomis* has retuse receptacles.

*Perula retusa* represents one of Rafinesque's attempts to break up the huge genus of *Ficus*. *F. retusa* was the type of his genus *Perula*.

Miquel's synonyms. Since Gasparrini's *Urostigma retusam* cited no author for the specific name that combination is credited to Miquel.

The classification of *U. ovoideum* as a synonym of *F. retusa* has been made by several authors, including King, but is perplexing, since most of its synonyms and references cited by Miquel belong to other species. The specific name was derived from Jack<sup>24</sup>, and from a specimen named *F. ovoidea* Jack which was listed in Wallich's catalog as no. 4526 (incorrectly stated by Miquel as no. 4524). These references have been declared by King (1887-1888; 1: 51) to be a form of *F. diversifolia* Blume. The citation which has directed *U. ovoideum* towards *retusa* is Miquel's of Wallich's no. 4530 B, which Wallich placed under *F. retusa*. This Miquel had not seen, but it is confirmed as *F. retusa* by King and others. In 1859 (1<sup>2</sup>: 345) Miquel said that *U. ovoideum* was like *U. nitidum*, but in 1867 he listed it as a separate variety of *F. retusa*. According to his descriptions it seems to be an intermediate form between var. *typica* and var. *nitida*, and here is placed under the former.

*F. dilatata* Miq. is listed as a synonym of *F. retusa* by King. Miquel's description obviously is of var. *typica* and states that it is near *F. retusa*.

*U. accedens*  $\beta$  *latifolia* was cited by Miquel (1867; 3: 288) as a synonym of *F. dilatata*.

*Retusa* forms mentioned by Koorders & Valeton. These authors, who

<sup>24</sup> Malay Misc. 2: 71. 1820-1822. Reprinted in Calcutta Jour. Nat. Hist. 4: 224-225. Ap. 1843.

usually accepted King's judgments on *Ficus*, did not think highly of his identifications of Javan specimens of *F. retusa*. They said (1906, 11: 113) that King determined a five-fold example in Koorders' herbarium as *F. retusa* forma *typica*, although only one specimen was *F. retusa*, and that differed from var. *nitida* only in wider leaves. Of the other specimens two were *F. indica* (Miquel's *F. indica*, see above), and two were *F. calophylla* Blume. On p. 38 Koorders & Valetton had said much the same about King's identification of *F. retusa genuina*. They quoted (p. 114) a statement by Koorders that var. *nitida* was the only Javan form in which secondary trunks were formed from air roots and from branches which forced themselves into the ground, rooted, and made new trunks.

*F. retusiformis* Lévillé has been definitely allocated to *F. retusa* by Rehder.<sup>35</sup> It was described from south China.

Haines' synonym is in incorrect form, but was made to differentiate the typical variety from var. *nitida*, which he also mentioned.

#### INCORRECT OR DOUBTFUL ALLEGED SYNONYMS OF SOME FORM OF *F. RETUSA*

*F. benjamina* Lour. = *F. benjamina* var. or ?*F. indica* Miq.

*F. cotoneaeifolia* var. *b.* Roem. & Schult. = ?

*F. indica* var. Lam. = ?

*F. indica fructu et foliis minoribus* Plum. MS 7, no. 109 ex Lam. = ?

*F. leptocarpa* Steud. = ? *F. ramentacea* Roxb.

*F. littoralis* Blume = ? *F. retusa* var. *typica*.

*F. magnoliifolia* Blume = *F. nervosa* Heyne ex Roth.

*F. microcarpa* var. *littoralis* (Blume) Blume = ? *F. retusa* var. *typica*.

*F. naumannii* Engl. = *F. retusa* according to Schumann & Lauterbach, but receptacles are peduncled and flowers do not agree.)

*F. ovoidea* Jack = *F. diversifolia* Blume.

*F. pyrifolia* Burm. f. = *F. erecta* Miq.

*F. retusa* var. *macrocarpa* Kurz. (King could not identify this.)

*Itty-Alu* Rheede = *F. benjamina* L.

*Urostigma littorale* (Blume) Miq. = ? *F. retusa* var. *typica*.

*Varinga parnifolia* alt. Rumph. = *F. benjamina* L.

*Varinga rubra* Rumph. = ?, near *F. calophylla* Blume.

#### SUMMARY

The close relationship between *F. retusa* L. and *F. nitida* Thunb. was not recognized in botanical literature until almost one hundred years after their publication. For more than 50 years after the latter was published by Miquel as a variety of the former no legal varietal name was given to distinguish the type of *F. retusa*.

Of the two varieties *nitida* seems to be the commoner and the more widely distributed, as well as the more distinctive. It is differentiated from var. *typica* by its leaves with their cuneate base and short blunt acumen, and also by the secondary trunks produced from its aerial roots. The latter aid in its propagation, and so in its artificial distribution. Both varieties are found in India, Malaya, south China, and the islands of the south-

<sup>35</sup> Jour. Arnold Arb. 17: 74. 1936.

western Pacific Ocean; but var. *typica* seems to have a wider natural distribution in peninsular India, and var. *nitida* is much more prominent in Java.

*F. retusa* sometimes is confused with another common East Indian fig-tree, *F. benjamina* L., which, however, is differentiated from it by its habit and leaves. The branches of *F. benjamina* droop, and the scanty aerial roots do not form trunks. The leaves have a broad base, an apex with a triangular and sometimes twisted acumen about 1 cm. long, inconspicuous basal veins, and numerous fine, parallel, lateral veins.

From the many synonyms of *F. retusa* those belonging to each variety have been selected, evaluated and segregated, usually with the help of such authorities as Miquel, King, and Warburg. Some synonyms have been rejected, and some homonyms have been removed from the host of names associated with the species. New descriptions from living trees of var. *nitida* in Florida and from texts and herbarium specimens of both varieties have been made.

MONTCLAIR, NEW JERSEY

## TORREYA

## PROCEEDINGS OF THE CLUB

**Minutes of the Meeting of May 4, 1948.** The meeting, at Columbia University, was called to order at 8:10 P.M. by President Small; 37 members and friends were present. The minutes of the preceding meeting were read and approved.

The following were elected to membership in the Club: Active Members: Paul R. Burkholder, New Haven, Conn.; Alexander Christoff, Sofia, Bulgaria; Bento Dantas, Pará, Brazil; Arshalus Demerjian, Yonkers, N. Y.; Regina M. Duffy, Jersey City, N. J.; Frederick D. Inge, Hampton, Va.; Peklo Jaroslav, Prague, Czechoslovakia; George H. M. Lawrence, Ithaca, N. Y.; Robert S. Lowry, E. Lansing, Mich.; Marjorie Mutchler, Bayonne, N. Y.; Jaques Rousseau, Montreal, P. Q.; Roy Stutzman, Prescott, Wis.; Associate Members: C. Raymond Brodix, New York, N. Y.; Mrs. Marshall D. Harrington, Madison, N. J.; Sylvia Stein, New York, N. Y.; Sophie K. Wolf, Brooklyn, N. Y.

Dr. W. J. Robbins of The New York Botanical Garden then gave his "Observations on a trip to Japan"—an account of some of the experiences of a group of six scientists (of whom he was one) sent to make a study of the organization of science in Japan, with a view to its being rendered more democratic.

The meeting was adjourned at 9:25.

**Minutes of the Meeting of May 19, 1948.** The meeting was called to order by President Small at 3:00 P.M. at the Boyce Thompson Institute for Plant Research; 53 members and friends were present. Dr. P. W. Zimmerman, who had arranged the program, presented time-lapse motion pictures of plant movements. Demonstrations and discussions were provided of submerged growth of mushroom mycelium, preparation of insecticides from essential oils, methods of measuring O<sub>2</sub> consumption and CO<sub>2</sub> production, methods of increasing duration of life of pollen, seed dormancy, effect of various substances on plant growth, and methods of evaluating fungicides. At the conclusion the club visited the grounds, especially to see the planting of tree peonies. No business was transacted.

**Minutes of the Meeting of October 5, 1948.** The meeting, at Hunter College, was called to order by President Small at 8:15 P.M.; about 40 members and friends were present. The minutes of the two meetings preceding were read and approved.

The following names were presented for election to membership: Honorary Life Member, Michael Levine, New York, N. Y. Life Member, Joseph Monachino, New York, N. Y. Active Members: William H. Baker, Corvallis, Ore.; John B. Carpenter, Lima, Peru; C. W. Hesseltine, Pearl River, N. Y.; Henning Horn af Rantzien, Stockholm, Sweden; Barbara F. Palser, Chicago, Ill.; Mildred Pangburn, Hackettstown, N. J.; Karl Silberschmidt, São Paulo, Brazil. Associate Members: Ida Berleant, New York, N. Y.; Ruth A. Beyer, Philadelphia, Pa.; Barbara B. DeHondt, Bayside, N. Y.; Martha Dresner, New York, N. Y.; Marcia A. Everett, Belvidere, N. J.; Joan Feld, Brooklyn, N. Y.; Varian Fry, New York, N. Y.; Mary A. Gonshorel, Brooklyn, N. Y.; Marie A. McAleer, Flushing, N. Y.; Simon D. Messing, New York, N. Y.; Mrs. C. A. Miller, Summit, N. J.; John B. Sangree, Glassboro, N. J.; Helen J. Schwarz, New York, N. Y.; Francis E. Wiederspahn, Springfield, N. J.; Dominick A. Zolla, Madison, N. J. It was moved, seconded, and carried without dissent that they be elected.

The members present were then asked to report on botanical activities of the past summer. Dr. M. A. Johnson discussed the summer foray of the Club and the Botanical Society of America in New Jersey. Dr. M. F. Buell described a study of an undisturbed area of eastern deciduous forest in Minnesota. Dr. H. W. Rickett reported on his study of Bradbury specimens in England, and on the nomenclatorial conference at Utrecht. Dr. Lela Barton discussed briefly the views expressed at the Washington meetings of the A.A.A.S. on science and the outlook for civilization, and papers read at the Botanical Society meetings on embryo culture. Dr. H. H. Clum reported on the physiologists' meetings at Cincinnati, and on work there described on growth-promoting substances and weed-killers and on photoperiodism. Dr. G. H. Shull described seedling albino specimens of *Quercus macrocarpa*. Mr. James McGrath gave an account of a collecting trip to the southern Appalachians and southeastern coastal plain. Miss Lois Wenman described a visit to the Nevada mountains. Miss Hester Rusk reported observation of the opening of evening primrose flowers.

The meeting then rose for refreshments.

Respectfully submitted,

DONALD P. ROGERS,  
Recording Secretary

### NOTES

A new botanical journal has appeared; by name *Physiologia plantarum*. It is the official publication of the Scandinavian Society for Plant Physiology. It is announced as a quarterly, each issue to contain about 100 pages. Vol. 1, Fasc. 1, p. 1-112, was received in New York on 12 July 1948; Fasc. 2, p. 113-205, on 5 August. Eighteen articles are contained in these two parts, dealing with a variety of topics in plant physiology. A striking and (for us) convenient feature is that all are written in English, though they originated in Stockholm, Uppsala, Lund, Copenhagen, and Helsinki.

Another rare botanical work has been republished by the photo-offset method. It is Rafinesque's *Précis des découvertes et travaux somiologiques*. It contains a "Foreword" by E. D. Merrill, but in other respects follows faithfully the original edition of 1814, published in Palermo "aux dépens de l'auteur." (The page is slightly enlarged in the reproduction.) "In it appear [to quote Dr. Merrill] very abbreviated descriptions of 110 new species of animals in various groups . . . and 79 new species of plants, as well as various new genera in both groups." Only six copies are recorded in American libraries.

"Somiologie", it should be observed, was the name Rafinesque gave to the science of living bodies, embracing both botany and zoology; perhaps derived from *σῶμα*, *body*.

The original price charged by Rafinesque for his small volume was 25 cents. By 1947 the work had appreciated just 100,000 per cent—a copy having been offered for sale in that year for \$250. The reprint is priced at \$4.00, and is obtainable from Peter Smith, 321 Fifth Avenue, New York 16.

Guillermo Hernandez de Alba has collected and edited the letters of José Celestino Mutis, the celebrated botanical explorer of the "Nuevo Reino de Granadas" (Colombia and adjacent regions). Volume 1 of the collected letters, which contains also a portrait and biographical sketch of their author, has been issued by the Ministerio de Educación Nacional at Bogotá (1947), under the title *Archivo epistolar del sabio naturalista José Celestino Mutis* (or, on the spine, *Epistolario del sabio Mutis*; the running head of the pages is *Cartas del sabio Mutis*). It forms a bulky volume of xxiii + 307 pages.

Under the title *Orchids in retrospect* the Botanical Museum of Harvard University has published a collection of the botanical writings of Oakes Ames. The essays were assembled by his colleagues as a celebration of his golden anniversary as "scholar, teacher and administrator" at Harvard. The collection embraces 14 papers, a biographical sketch with portrait, and a list of publications of the distinguished student of Orchidaceae. The papers are drawn mainly from his more popular writings. Many of the superb illustrations drawn by Blanche Ames are included. The book (xix + 172 p.) is sumptuously printed on the finest paper, bound in heavy red paper.

## REVIEWS

**Beginner's Guide to Wild Flowers.** By Ethel Hickley Hausman. 376 p. G. P. Putnam's Sons, New York.

This conveniently small book is intended for "beginners," those who cannot or do not wish to use the available keys for identifying unknown plants. Here the wild flowers are divided into five color-sections. Within each section the flowers are arranged according to families. The idea, however is to thumb through the pages to find the drawing which corresponds to the flower in hand. It is further suggested that the drawing then be colored from the specimen and the paper has been selected to make this possible. This should have a real appeal to many amateurs (especially to children)—the attractiveness and usefulness of the book growing as the user becomes acquainted with more of the wild flowers. The drawings are neat and clear, showing flowers and leaves, often the entire plant. There are three on each page and 360 pages of them. Beside each is a very brief description giving common and botanical names, color variations, significant measurements, habitat, distribution, and family. The color-section heading is carried across the pages.

The reviewer tried out the book with three children 10 and 11 years of age, who gathered flowers they did not know and were successful in identifying all in a short time.—THERESA C. RICKETT.

**Advances in Genetics.** Edited by M. Demerec. Volume 1, xvi + 458 p. 1947. Volume 2, viii + 373 p. 1948. Academic Press, New York.

Between the journal paper, with its detailed consideration of specific small segments of a general problem, and the textbook, which can perforce contain only broad outlines, there has existed a large gap in genetic publications, filled only by occasional reviews. *Advances in Genetics*, of which Volumes 1 and 2 are the first of what should be a lusty family, in which new sibs will appear annually, is a praiseworthy and successful effort to fill this breach. Its editor, M. Demerec, indicates in the preface to Volume 1 that "critical summaries of outstanding genetic problems, written by competent geneticists . . . are expected to deal with both theoretical and practical problems, and to cover plant breeding, animal breeding, and human heredity, as well as the related fields of biophysics, biochemistry, physiology, and immunology. The aim is to have the articles written in such form that they will be useful as reference material for geneticists and also as a source of information to nongeneticists." The editor is assisted by an editorial board consisting of G. W. Beadle, W. C. Boyd, Th. Dobzhansky, L. C. Dunn, M. T. Jenkins, J. L. Lush, A. Mirsky, H. J. Muller, J. T. Patterson, M. M. Rhoades, L. J. Stadler, and C. Stern.

The reviews contained in the first two volumes amply fulfill the editorial aims. In many cases the reviewers are the persons most concerned with the modern development of their field. The treatment, which necessarily varies among the various writers, is suffi-



ciently specific to afford a good grasp of details without being so much so as to obscure the essential outlines of a problem. As is to be expected, those reviews which deal with controversial topics reveal some bias toward the reviewer's own convictions. The editor is to be congratulated on his choice of topics for inclusion, striking a balance between the standard, reviewed-to-death subjects and the less well known. An adequate subject index and an author index to cited researches are provided.

In Volume 1, Sanford S. Atwood discusses cytogenetics and breeding of forage crops, reviewing the cytology, genetics, and practical breeding of the more important forage grasses and legumes. Ernest B. Babcock reviews the cytogenetic processes involved in speciation in *Crepis*. Myron Gordon discusses speciation in fishes, giving an interesting analysis of the distribution in time and space of seven dominant multiple alleles in *Platyocellus*. In the general field of immunogenetics, M. R. Irwin reviews the work on the human cellular antigens, species relations as revealed by the antigens of doves, and the interesting antigen relations in cattle. P. C. Mangelsdorf attacks the vexing problem of the origin and evolution of maize; unfortunately he probably has not succeeded in satisfying any of the several opposing groups of doctrinaires interested in this subject. Robert R. Shrode and Jay L. Lush discuss the genetics of cattle, including the complexities of milk and beef production as well as the simpler morphological characters. The recent advances in the genetics of *Paramecium* and *Euplotes* are ably summarized by the man most responsible for them, Tracy M. Sonneborn, who points out the many possibilities of protozoa as genetic material. The occurrence and distribution of mutations in wild populations of *Drosophila* is discussed by Warren P. Spencer. G. Ledyard Stebbins, Jr. assesses the significance of polyploidy as an evolutionary process, and attempts to construct an orderly classification of the various types. The cytogenetics of *Gossypium* and the problem of origin of the New World cottons are reviewed by S. G. Stevens.

The opening review of Volume 2 is a discussion by Ernst Caspari of cytoplasmic inheritance, in which he covers a number of classical cases which have been lost to the public eye in the recent excitement over *Paramecium* and the yeasts. Gunnar Dahlberg applies to the genetics of human populations some of the concepts which have already yielded excellent results in the fruit-flies. W. E. Heston reviews the genetics of cancer. Sally Hughes-Schrader gathers together much information concerning the cytology of the coccids, a group which is a proving-ground for variations on the more common type of chromosome structure and behavior. Ernst Mayr discusses the nature of species in the light of the combined approach of the "new systematics." The cytology and genetics of the wheats and their relatives is reviewed by E. R. Sears. D. G. Catheside treats of the genetic effects of radiations.—J. R. SINGLETON.

# INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITOR OF THE TAXONOMIC INDEX

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used to include the entire Western Hemisphere.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the Bibliographer to errors or omissions, their kindness will be appreciated.

The Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of three cents for each card. The different subjects as classified below may be ordered separately (but no orders will be taken for less than one year's issue in any classification). Correspondence relating to the card issue should be addressed to the Treasurer of the Club.

## TAXONOMY, PHYLOGENY AND FLORISTICS

### ALGAE

(See also under Ecology and Plant Geography: Gessner)

- Flint, Lewis H.** Studies of fresh-water red algae. *Am. Jour. Bot.* **35**: 428-433. *f.* 1-40. *Jl* [Au] 1948.
- Hewitt, A. F. & Gustafson, P. V.** Plankton forms of some lakes near Spokane. *Northw. Sci.* **21**: 168. *N* 1947.
- Hughes, Elwyn, O.** New fresh-water Chlorophyceae from Nova Scotia. *Am. Jour. Bot.* **35**: 424-427. *f.* 1-6. *Jl* [Au] 1948.
- Northcroft, Richard D.** Marine algal colonization on the Monterey Peninsula, California. *Am. Jour. Bot.* **35**: 396-404. *f.* 1-6. *Jl* [Au] 1948.
- Tiffany, Lewis Hanford.** *Oedogonium chapmanii* sp. nov. from New Zealand. *Nat. Hist. Misc.* **16**: 1-3. *f.* 1-9. [*pl.* 1 on p. 3]. 15 Ap 1948.

### FUNGI AND LICHENS

(See also under Bryophytes. Gorham)

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## PRODUCTION OF PENICILLIN ON NATURAL MEDIA

D. PERLMAN

The production of penicillin on media which included natural materials as sources of nitrogen and other factors has received considerable attention during the past few years. Moyer and Coghill (20, 21) have reported studies where the inclusion of cornsteep liquor in a lactose-salts medium was found to increase the yields of penicillin markedly. Bowden and Peterson (3) have noted that under the conditions of their experiments "no satisfactory substitute for cornsteep liquor has been found," although the addition of other materials to the cornsteep liquor-lactose-salts medium resulted in some increase in antibiotic activity. More recently Cook and his associates (6, 7, 8) have observed that the addition of extracts of dried peas to a carbohydrate-salts medium increased the yields of penicillin in surface culture, and that gelatine and other factors may partially replace the pea extract. As the chemistry of the penicillins became known it was concurrently observed that the types of penicillin produced depend in part on the presence of certain compounds present in the medium which act as precursors leading to the production of penicillin G (benzylpenicillin) or other types (1, 4, 13, 19). Foster and his coworkers (9, 10) have reported that cottonseed meal and other materials may completely or partially replace cornsteep liquor in the medium without considerable reduction in penicillin yield (antibiotic potency). With cottonseed meal it was noted (10) that equivalent yields of penicillin were obtained with or without the addition of a penicillin G precursor to the medium (of the general types mentioned in 13 and 23), while much lower yields were obtained on the cornsteep liquor medium when the precursor was not added.

The studies reported here indicate that several other proteinaceous materials may be substituted for the cornsteep liquor in media for the production of penicillin without marked change in penicillin yield. When these studies were completed early in 1946 the elegant analytical methods for the quantitative and qualitative estimation of penicillin in fermentation broths recently described by Prof. Johnson (16) were not available and thus it is not known whether the same penicillins are produced on all these media. From the recent report by Jarvis and Johnson (14) on penicillin production on synthetic media it appears probable that the bulk of the antibiotic activity on a natural medium supplemented with a penicillin G precursor will be penicillin G if the Wisconsin Q<sub>176</sub> strain of *Penicillium*

*chrysogenum* is used. It is interesting to note that the potencies mentioned (in the following experiments) are of the order of 0.5 mg. per ml. or approximately 1 per cent of the total solids present in the crude broth, a purity related by Chain (5) as equivalent to that used in the early therapeutic tests.

**Methods.** The analytical methods used in these studies were in the main those described by Koffler and associates (17). The culture of *P. chrysogenum* Wis. Q<sub>176</sub> (described by Backus et al., 2) obtained from Prof. M. P. Backus was cultured on the medium mentioned by Gailey and others (11) as being optimal for *P. chrysogenum* Demerec X 1612. The fermentations were carried out at 22–24° C. in cotton plugged 250 ml. Erlenmeyer flasks containing 80 ml. of medium. After inoculation these flasks were placed on rotary shaking machines (220 rpm) mentioned by Foster and others (9). A vegetative inoculum was used in all experiments, and was prepared (unless otherwise indicated) by inoculating flasks containing a medium consisting of the indicated nitrogenous material (at 2 per cent solids concentration) and 2 per cent glucose (or other carbohydrate as indicated) with approximately 1 ml. of a spore suspension prepared as described by Gailey and others (11). After approximately 48 hrs. incubation on the shaking machines ca. 2 ml. of the vegetative growth (resembling paper pulp) was added to each of the fermentation flasks. There were usually three or more replicate flasks of each experiment. The flasks were sampled daily after the third day of incubation until assays on two consecutive days had indicated that a maximum yield had been reached. Each flask was sampled and assayed individually, and the results from replicate flasks were averaged. In the results presented in table 3 duplicate flasks were removed at the end of the indicated fermentation period and the contents were pooled before analysis. Control flasks containing cornsteep liquor–lactose medium were included with each group of fermentations to check for peculiarities in behavior of the fermentations that might be attributed to cultural abnormalities. Gailey and his associates (11) have reported that the penicillin yields may vary considerably with a given culture on a given medium, and in the course of these experiments the yields ranged from 1350 U. per ml. to 950 U. per ml. on the cornsteep liquor medium. Accordingly any yield in the vicinity of 1000 U. per ml. has been considered as good. Unless otherwise indicated the medium used in all fermentations contained (per liter): calcium carbonate, 10 g.; soybean oil, 3.2 ml.; and tap water q.s. one liter. All flasks were autoclaved at 120° C for 20 minutes. The other ingredients of the media were obtained from various commercial sources. The penicillin G precursor added was similar to those mentioned in the literature (1, 12, 13, 18, 23).

**Experiments.** The results obtained when a number of naturally occurring proteinaceous materials were substituted for the cornsteep liquor in the medium mentioned above are summarized in table 1. Several concentrations of each substance were tested as indicated, in media with and without the added penicillin G precursor. While considerable data were collected in these experiments only the maximum yields of antibiotic activity are noted in order to make the comparisons clear. In most cases when the concentration of proteinaceous material was increased to 40 grams per liter the resulting mycelial growth was so voluminous that no doubt the aeration and agitation were impaired and consequently the same aerobic conditions did not exist in these flasks that were obtained in the others containing less of these materials. This is thought to account for the lowered penicillin yields found in certain cases, and undoubtedly under higher and more efficient aeration the yields would be higher as deduced from the results obtained by Bowden and Peterson (3). It will be seen that with certain materials including yeast extract very poor yields were obtained. In these fermentations the pH rose quickly to 7.8 and shortly thereafter to 8.5 indicating that perhaps autolysis was occurring, an observation confirmed by the odor of ammonia which has been associated with the autolytic phase of the fermentation by Koffler and others (17) who reported that little penicillin is usually found under these conditions.

The previous history of the inoculum was thought to have some importance in the results obtained by Foster and his coworkers (10). The importance of this factor in these studies is summarized in table 2 where the data obtained in several experiments are collected. The carbohydrate source present in the inoculum medium was varied between lactose, mannitol, starch, inulin, sorbose, xylose, and glucose. These have been used in previous studies.<sup>1</sup> A number of proteinaceous materials included cornsteep liquor, cottonseed meal, linseed meal, and menhaden meal. The carbohydrate source in the inoculum medium seems to have some effect, but not as much as the nitrogen source. For example, if the inoculum was grown on a menhaden meal—glucose medium lower yields were obtained during the fermentation than if it were grown on a cornsteep liquor—glucose medium. Thus, while faster growth was observed on the cottonseed medium (Foster et al., 10), it would not be the best inoculum to use to inoculate fermentation media containing other nitrogen sources.

A considerable number of studies have been reported on the chemical changes occurring during the penicillin fermentation (reviewed by Johnson, 15). Some of the data collected during these experiments are presented in table 3. It will be seen that the penicillin yields on the three

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<sup>1</sup> D. Perlman, Ph.D. Thesis, University of Wisconsin, 1945.

TABLE 1. *Production of Penicillin on Natural Media.*

Substance substituted for cornsteep liquor <sup>a</sup>	g./l	Maximum penicillin production	
		Without precursor U./ml.	With precursor U./ml.
Cornsteep liquor (solids)	20	650	1300
	30	580	1050
	40	400	800
Cottonseed oil meal ..	30	800	1200
	40	1000	1160
Linseed oil meal .....	20	700	1035
	40	635	1100
	60	.	570
Coconut oil meal	60	450	1150
	90	500	810
	120	300	680
Sardine meal	10	150	610
	20	400	900
	30	575	1130
Rape seed oil meal	10	150	340
	20	180	450
	30	285	515
	60	730	705
	90	335	615
Peanut oil meal	10	300	710
	20	600	630
	30	950	900
	40	1050	1350
Mustard flour	30	650	980
	40	590	1060
Dried peas (split)	20	345	305
	30	280	250
	40	250	240
Dried beet crowns	50		90
	100		90
	150		75
Yeast extract (Difco)	30	..	45
	60	.	40
	90		55
Peptone (Bacto)	30	400	750
	60	50	90
	90	45	90
Soybean oil meal (expeller) ....	20	305	1030
	40	170	930
Castor bean meal .....	20	780	390
	40	460	430
Menhaden meal . . . . .	20	780	390
	40	460	430

TABLE 1 (Cont.)

Substance substituted for cornsteep liquor <sup>a</sup>	g./l	Maximum penicillin production	
		Without precursor U./ml.	With precursor U./ml.
Fish meal (mixed)	20	830	430
	40	540	790
Poppy seeds	20	180	275
	30	270	320
	40	265	440

<sup>a</sup> Other ingredients included 30 g. lactose and 1 g. penicillin G precursor (where indicated), 3.2 ml. soybean oil, and 10 g. calcium carbonate per liter.

media are approximately equal, and that many of the changes found were the same in the three media. The pH did not rise as high in the cottonseed meal and linseed meal media as it did in the cornsteep liquor medium, but of course these materials did not contain the lactate present in the latter medium (Koffler et al., 17). The mycelium weights were greater on the cottonseed meal and linseed meal media than on the cornsteep liquor medium, but may have been incorrect since visual observation indicated that the meal was not completely disintegrated in those media until after the third and fourth days of the fermentation. The lactose fermentation in the linseed media was somewhat slower than in the other two media. Respiration measurements indicated that the oxygen demands were approximately the same on all three media. The nitrogen in solution (Kjeldahl) data were undoubtedly affected by the slow breakdown of the protein matter in the linseed and cottonseed meal media and are consequently incorrect. Cornsteep liquor is relatively high in inorganic phosphorus while the cottonseed meal and linseed meal are relatively low. However, a few determinations indicated that there was evidently enough phosphate present that some was found in the mycelium-free medium. Another observation indicated that the mold hydrolyzed the proteinaceous material fairly rapidly as indicated by the disappearance of the particles of meal, and also by the presence of soluble nitrogen in the solution during the fermentation, and a crude assay for extracellular proteinase indicated that, as might be expected, the extracellular proteinase production was highest in the media containing the unhydrolyzed protein.

**Discussion.** These few experiments have tended to confirm the reports by others (7, 10, 14) that penicillin production on cornsteep liquor containing media is not a result of something intrinsically special about this substance, since cottonseed meal, linseed oil meal, castor bean oil meal, and many other proteinaceous materials can be substituted for the cornsteep



liquor without reduction in penicillin yields. It is probable that the advantage of cornsteep liquor may be associated with its phenylalanine and phenylethylamine constituents (19) and the phenylalanine content of other products is as high as that found in cornsteep liquor. It is interesting to note that with a number of materials the yields of penicillin with and without added penicillin G precursor were approximately equal, e.g. media prepared with cottonseed meal, rape seed oil meal, peanut oil meal, and dried peas. Whether or not the same penicillins were produced under these conditions was not determined. According to Johnson (16) this organism produces mainly those penicillins with aliphatic side chains in synthetic media (14), and penicillin G production is associated with the presence of a phenyl acetyl derivative, or a substance yielding phenylacetyl derivatives during the fermentation.

Under the conditions of these experiments several materials which have previously been reported by others as satisfactory for inclusion in media for the production of penicillin have not yielded very satisfactory results, e.g. dried peas. On the other hand Ulkin (22) reported that peptone was definitely unsatisfactory, and in these experiments it was fairly good as a replacement for the cornsteep liquor in media supplemented with the penicillin G precursor. Undoubtedly the great differences in experimental conditions account for the disagreement in results between these different laboratories.

The experiments on the effect of history of inoculum on penicillin production are somewhat inconclusive. Evidently under certain conditions the

TABLE 2. *Effect of Inoculum Medium Composition on Penicillin Production.*

A. Nitrogen source Inoculum medium <sup>a</sup>	Fermentation medium <sup>b</sup>	Maximum penicillin production U./ml.
Cornsteep liquor	Cornsteep liquor	880
	Linseed oil meal	750
	Cottonseed oil meal	775
	Menhaden meal	570
Cottonseed meal	Cornsteep liquor	730
	Linseed oil meal	540
	Cottonseed oil meal	830
	Menhaden meal	585
Linseed oil meal	Cornsteep liquor	865
	Linseed oil meal	790
	Cottonseed meal	740
	Menhaden meal	460
Menhaden meal	Cornsteep liquor	350
	Linseed oil meal	600
	Cottonseed meal	900
	Menhaden meal	630

TABLE 2.—Continued

<i>B. Carbohydrate source.</i> Inoculum medium carbohydrate <sup>c</sup>	Fermentation medium <sup>d</sup>	Maximum penicillin production U./ml.
None	Lactose—cottonseed meal	910
	Lactose—peanut oil meal	765
	Mannitol—peanut oil meal	765
Glucose	Lactose—cottonseed meal	850
	Lactose—peanut oil meal	735
	Mannitol—peanut oil meal	800
Lactose	Lactose—cottonseed meal	960
	Lactose—peanut oil meal	695
	Mannitol—peanut oil meal	700
Mannitol	Lactose—cottonseed meal	835
	Lactose—peanut oil meal	760
	Mannitol—peanut oil meal	725
Starch	Lactose—cottonseed meal	950
Inulin	Lactose—cottonseed meal	1055
Sorbose	Lactose—peanut oil meal	880
	Mannitol—peanut oil meal	825
Xylose	Lactose—peanut oil meal	660
	Mannitol—peanut oil meal	860

<sup>a</sup> Cornsteep liquor: 20 g. cornsteep liquor solids; 20 g. glucose; tap water q.s. 1 liter.

Linseed oil meal: 20 g. linseed oil meal; 20 g. glucose; tap water q.s. 1 liter.

Cottonseed meal: 20 g. cottonseed meal; 20 g. glucose; tap water q.s. 1 liter.

Menhaden meal: 20 g. menhaden meal; 20 g. glucose; tap water q.s. 1 liter.

<sup>b</sup> Cornsteep liquor: 20 g. cornsteep liquor solids; 30 g. lactose; 1 g. penicillin G precursor; 3.2 ml. soybean oil; tap water q.s. 1 liter; 10 g. calcium carbonate.

Linseed oil meal: 40 g. linseed oil meal; 30 g. lactose; 1 g. penicillin G precursor; 3.2 ml. soybean oil; tap water q.s. 1 liter; 10 g. calcium carbonate.

Cottonseed meal: 30 g. cottonseed meal; 30 g. lactose; 1 g. penicillin G precursor;

3.2 ml. soybean oil; tap water q.s. 1 liter; 10 g. calcium carbonate.

Menhaden meal: 30 g. menhaden meal; 30 g. lactose; 1 g. penicillin G precursor;

3.2 ml. soybean oil; tap water q.s. 1 liter; 10 g. calcium carbonate.

<sup>c</sup> Inoculum medium: 20 g. indicated carbohydrate; 20 nitrogenous material (as in fermentation medium); tap water q.s. 1 liter.

<sup>d</sup> Fermentation medium: 30 g. lactose or mannitol as indicated; 40 g. cottonseed meal or peanut oil meal as indicated; 10 g. calcium carbonate; 3.2 ml. soybean oil; tap water q.s. 1 liter. (Note: no penicillin G precursor was added to these media.)

addition of no carbohydrate to the inoculum medium is better than other combinations. The nitrogenous material present in the inoculum phase is perhaps much more important than the carbohydrate in determining the penicillin yields in the fermentation medium, and evidently care should be taken to make sure that certain combinations are not used.

The few studies on chemical changes occurring during the fermentation tend to indicate that the same general changes occur in media containing the cottonseed meal and linseed oil meal instead of the cornsteep liquor. Perhaps under other fermentation conditions significant differences

would be found between the changes occurring during the fermentation of the three media, and the standardization of procedure has limited the number of satisfactory replacements for the cornsteep liquor. It is not

TABLE 3. *Chemical Changes Occurring During the Fermentation of Natural Media.*

Medium <sup>a</sup>	Duration of fermentation					
	0 day	2 days	3 days	4 days	5 days	6 days
Penicillin Production (U./ml.)						
Cornsteep liquor		690	1100	1450	1170	1020
Cottonseed meal		550	980	1350	1190	900
Linseed oil meal		400	900	1300	1140	1150
pH						
Cornsteep liquor	6.70	7.20	7.25	7.45	8.25	8.45
Cottonseed meal	6.35	6.80	7.15	7.70	7.35	7.55
Linseed oil meal	7.00	7.15	7.20	7.05	7.40	7.60
Mycelium Weight (mg./ml.)						
Cornsteep liquor		24	26	22	23	19
Cottonseed meal			30	33	30	31
Linseed oil meal				33	30	29
Lactose (mg./ml.)						
Cornsteep liquor	29	16	9	3	4	3
Cottonseed meal	31	18	11	6	7	5
Linseed oil meal	27	20	18	10	7	3
Oxygen Demand (Q <sub>O<sub>2</sub></sub> /ml.)						
Cornsteep liquor		84	75	62	55	38
Cottonseed meal			65	68	50	48
Linseed oil meal				58	60	50
Nitrogen (Kjeldahl) in Solution (mg./ml.)						
Cornsteep liquor	2.25	1.24	1.04	1.39	1.48	1.58
Cottonseed meal	1.60	1.75	1.00	0.90	0.70	1.10
Linseed oil meal	1.90	1.60	1.05	0.95	0.80	0.90

<sup>a</sup> Composition of media: *Cornsteep liquor*: 20 g. cornsteep liquor solids; 30 g. lactose; 10 g. calcium carbonate; 1 g. penicillin G precursor; 3.2 ml. soybean oil; tap water q.s. 1 liter.

*Cottonseed meal*: 30 g. cottonseed meal; 30 g. lactose; 10 g. calcium carbonate; 1 g. penicillin G precursor; 3.2 ml. soybean oil; tap water q.s. 1 liter.

*Linseed oil meal*: 40 g. linseed oil meal; 30 g. lactose; 10 g. calcium carbonate; 1 g. penicillin G precursor; 3.2 ml. soybean oil; tap water q.s. 1 liter.

surprising that synthetic media based in part on the composition of cornsteep liquor have been found to give nearly as high penicillin yields as are obtained with the cornsteep liquor medium (14).

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#### SUMMARY

A number of natural materials have been found to replace cornsteep liquor in the penicillin production medium. These include cottonseed meal, linseed oil meal, coconut oil meal, sardine meal, peanut oil meal, mustard flour, soybean oil meal, and perhaps castor bean meal. The composition of the inoculum medium has a pronounced effect on the fermentation. The gross chemical changes occurring during the fermentation of media prepared with cornsteep liquor, linseed oil meal, and cottonseed oil meal are quite similar.

PRINCETON, NEW JERSEY.

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ATKINSIA GEN. NOV., THESPESIA, AND RELATED WEST  
INDIAN GENERA OF THE MALVACEAE<sup>1</sup>

RICHARD A. HOWARD

In a recent issue of the New Phytologist (46: 123-141. 1947) J. B. Hutchinson has published a study entitled "Notes on the classification and distribution of genera related to *Gossypium*." His paper concerns a group of genera suggested as a division of the Hibisceae of the Malvaceae, with "rounded, compressed or turbinate seeds and with the styles usually joined and clavate and only rarely free or capitate." In his paper, Hutchinson has placed the West Indian genera, *Montezuma* Sessé & Mocino, *Maga* Urban, and *Armouria* Lewton, in the synonymy of the genus *Thespesia* Solander, including them by expanding the generic limits of the genus *Thespesia*. I can not agree with Hutchinson's conclusions and in this paper will separate the native West Indian species from *Thespesia* and maintain them as species in monotypic endemic genera.

There are superficial similarities which hold the genera together in a general complex, but there are striking differences between the various species occurring in the West Indies which I feel Hutchinson does not evaluate properly. Certainly the circumscissile deciduous calyx of *Thespesia grandiflora* is strikingly different from anything else in the genus as characterized by Hutchinson. *Thespesia cubensis* is readily distinguished by the shortened leafless terminal spike of flowers, the short corolla exceeded by the staminal column, the persistent woody calyx, and the domatia in the axils of the primary veins. *Thespesia beata* is distinct with a loculicidally dehiscent capsule, lobed and densely pubescent leaves, and the calyx investing the mature capsule.

It is my opinion that these differences between many of the species of *Thespesia* as treated by Hutchinson are as great as or greater than the differences between other genera in his treatment of this division of the Hibisceae. Most of the genera of Hutchinson's treatment are small and readily characterized. I can see no reason for expanding the genus *Thespesia* to become a catch-basket. I therefore propose to follow the earlier treatments of Urban, Britton and Lewton and maintain the West Indian species, which Hutchinson calls *Thespesia grandiflora*, *T. cubensis*, and *T. beata*, as the type species of monotypic genera on the strength of the characters given in the key below.

In addition errors have crept into Hutchinson's work. He apparently did not see any herbarium material of *Thespesia cubensis* nor did he read

<sup>1</sup> Publication No. 4. Journal Series from the Atkins Garden and Research Laboratory of Harvard University, Soledad, Cienfuegos, Cuba.

Urban's comments on this species (as *Maga cubensis*) published in Fedde Repert. Sp. Nov. **24**: 237 (1928). The original description of this species does not agree with the type specimen and this discrepancy was noted by Urban. It can be readily observed from the numerous collections of this species, in addition to the type collection, that the calyx is not circumscissile but woody and persistent. It was on the supposed character of a "circumscissile" calyx that Britton and Wilson placed the species in the genus *Maga* [= *Montezuma*] and this erroneous character is still used by Hutchinson to place *T. cubensis* in his key.

The material referred to as *Maga cubensis* by Britton and Wilson is a distinct species and can not be accommodated in *Thespesia* or *Montezuma*. A new genus is established for this species in the present paper.

Hutchinson also overlooked the genus *Ulbrichia* Urban, based on material collected by Ostenfeld on Beata Island near the Dominican Republic. The material is identical with that collected by Fairchild and Dorsett on the same island; which is the type of *Armouria beata* Lewton. Urban's new genus and species *Ulbrichia beatensis*, antedates *Armouria beata* by nine years.

After the endemic West Indian species have been removed from Hutchinson's amended *Thespesia*, the genus contains five species. The species typifying the genus, *T. populnea*, is a pantropical coastal weedy tree. The fruits are used medicinally throughout the tropics. The flowers are eaten for food and the tree itself is planted as a shade or ornamental tree. Its widespread use as a cultivated plant for coastal areas is a result of its tolerance to salt spray. Two species are found in Africa, *T. danis* Oliver and *T. garckeana* F. Hoffm. I have not seen any material of *T. danis* and can find no elaboration of the original description and plate of the plant in flowering condition. Certainly the position of the bracteoles (Hook. Ic. **14**: pl. 1336. 1881) high on the calyx is unusual for *Thespesia*. A fourth species, *T. lampas* Cav. is widely used as an ornamental. It is reported as introduced into the Philippines, Java, and Jamaica. It is also reported from Ceylon and India, Burma, Siam, Indo-China, the Celebes, and Hawaii. It is probably native in India where it occurs as a forest shrub. *Thespesia lampas* has been considered distinct from *Thespesia* and was proposed as the type species of the genus *Azanza* by Alefeld (Bot. Zeit. **19**: 298. 1861). It has been accepted as a distinct genus by several recent authors. The last species left in Hutchinson's treatment is *Thespesia tomentosa* Presl. from Western Mexico, apparently known only from the original description. Standley does not mention this species in his *Trees and shrubs of Mexico*. *T. tomentosa* appears to be similar to *Ulbrichia beatensis* in its pubescence but has 8 bracteoles compared with 3 in *Ulbrichia*.

For a discussion of the problem of limitation of the genus *Thespesia* and for notes on the original description, see the article by Baker entitled "Notes on *Thespesia*" (Jour. Bot. **35**: 50-54. 1897).

Several morphological characters found generally in the Malvaceae and in this group of West Indian genera merit further comment. Frequently, in the Malvaceae, the calyx is pubescent on the inside as well as the outside. The genera considered in this paper have a cupular calyx usually truncate at the apex. The pubescence inside the calyx is very dense on all specimens I have seen, yet this character is not mentioned in most of the earlier descriptions. The pubescence consists of lepidote-stellate hair clusters with the free arms of the cluster often very long and giving the impression of a dense tomentum of individual hairs.

Urban paid considerable attention to the shape of the ovary and fruit and the number of locules in his generic descriptions. The ovary is 5-celled but usually only 3 or 4 of the locules will mature seeds. The other locules may be enlarged so that the fruit is symmetrical or the locules may be collapsed and not at all evident giving an asymmetrical fruit. The ovules are attached at the base and careful dissection will usually show the abortive seeds near the base of the fruit.

As is typical in many of the Malvaceae, punctate lines or dots are found on many parts of the plant in the species considered in this paper. The calyx is usually heavily black-dotted and at times the resinous material may exude in drying so that the fruiting calyx will be filled, around the capsule, with black resinous droplets. The petals may have numerous black lines or dots, associated with the veins or aggregated near the upper margin of the petal. The inner layers of the fruit may be filled with resin-bearing cells. Urban, after dissecting seeds, distinguished between several genera on the presence or absence of black dots in the cotyledons. I have examined most of the material cited by Urban plus many other specimens of all the species cited in this study and have found resin-bearing cells in the cotyledons of all seeds examined.

The author is grateful to the curators of the following herbaria for material examined in the course of this survey: Gray Herbarium (G), The New York Botanical Garden (NY), and the United States National Herbarium (US).

Calyx circumscissile in fruit; ovary glabrous; [seeds glabrous].

*Montezuma.*

Calyx persistent in fruit; ovary lepidote or lepidote-stellate.

Calyx expanded in fruit, flat, recurved or undulate; [staminal column shorter than the corolla; capsule indehiscent;] seeds pubescent.

*Thespesia.*

Calyx cupular, enclosing the fruit, entire or broken; seeds glabrous.

Calyx cupular, half investing the capsule, entire; staminal column shorter than the corolla; flowers solitary, axillary to the leaves; capsule loculicidally 5-valved.

*Ulbrichia.*

Calyx expanded and broken in fruit; staminal column exceeding the corolla [1.5-3 times as long]; flowers in shortened terminal leafless spikes; capsule indehiscent.

*Atkinsia.*



## MONTEZUMA Sessé &amp; Moc.; DC. Prodr. 1: 477. 1824.

*Maga* Urban, Symb. Ant. 7: 281. 1912.

Trees. Leaves alternate, petiolate, entire or slightly undulate, broadly ovate, cordate. Stipules small, deciduous. Flowers solitary in the axils of leaves, on simple peduncles. Involucre of 3 small, linear, deciduous bracts. Calyx subcampanulate truncate, circumscissile at the base after flowering, deciduous. Petals 5, large, united at the base. Staminal column united at the base with the corolla, scarcely as long as the petals. Stigmas united, clavate. Ovary sessile, glabrous, 5-celled, ovules about 5 in each locule. Capsule fleshy, becoming woody when dry, thick, indehiscent. Seeds glabrous, cotyledons black-punctate.

MONTEZUMA GRANDIFLORA (DC) Urb.; Urb. & Helwig, Repert Sp. Nov. 24: 238. 1928. (Figs. 1-6). *Thespesia grandiflora* DC. Prodr. 1: 456. 1824. *Maga grandiflora* Urb. Symb. Ant. 7: 281. 1912. *Montezuma speciosissima* Sessé & Moc.; DC. Prodr. 1: 477. 1824. Urb. Notizbl. 7: 543. 1921.

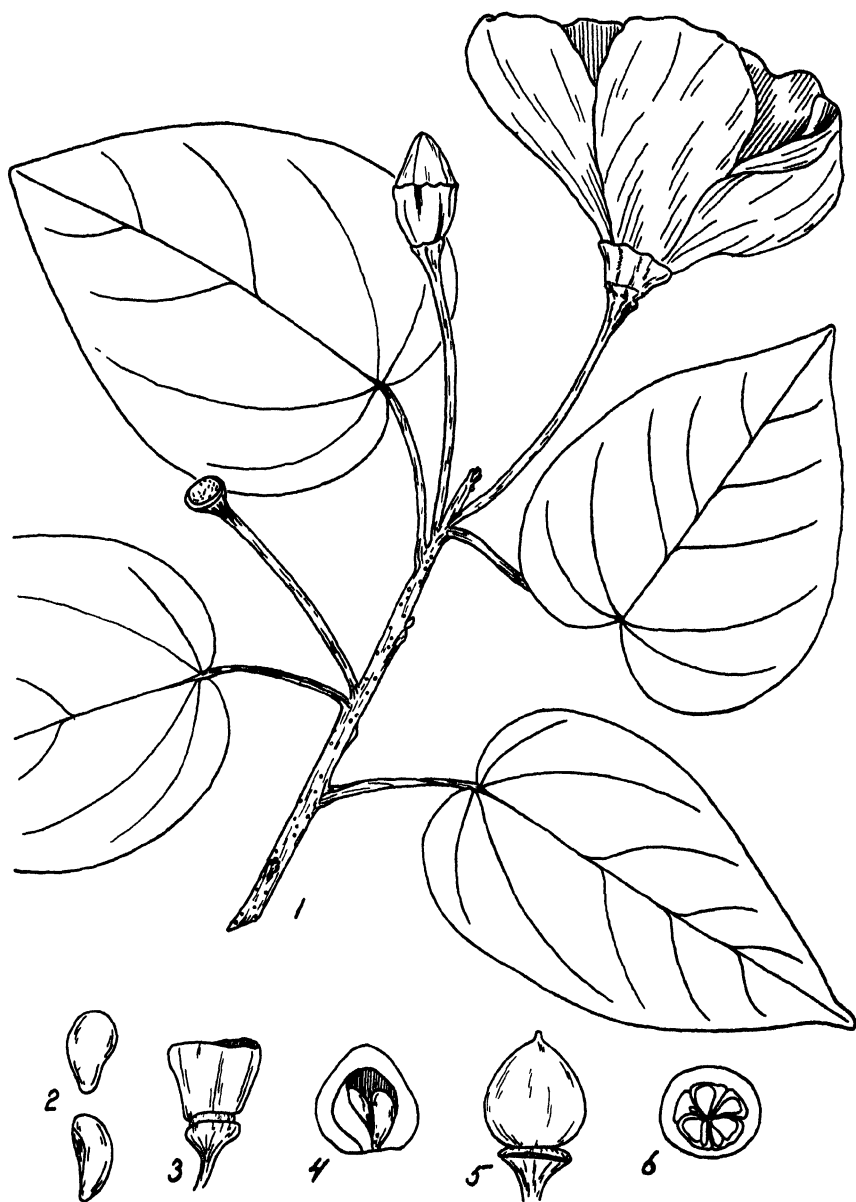
Tree to 15 m. tall; young branches stout, lepidote-stellate-pubescent; stipules linear-subulate, 3-4 mm. long, deciduous; leaves orbicular-ovate, 5-25 cm. long (4) 8-19 cm. broad, apex acuminate or acute, base cordate rarely subtruncate, the lobes often overlapping, margin entire to undulate, sparsely lepidote-stellate on both sides when young, especially at the base of the blade; palmately 5-7-nerved; petioles 3-18 cm. long, lepidote-stellate; peduncles 6-25 cm. long, lepidote-stellate, bracteoles 3, linear, 1.8 cm. long, 1.5 mm. broad, caducous; calyx cyathiform or subcampanulate, 1.7-2.5 cm. long, 1.5-2 cm. diameter in flower, truncate at the apex, minutely lepidote-stellate outside, densely long-tomentose inside, the hairs usually clustered; petals obliquely triangular-obovate, 7-11 cm. long, 5-7.5 cm. broad, deep rose shading to crimson inside, orange or tan outside, with black dots or lines along the veins in the center of the petal, densely lepidote-stellate to tomentose outside, glabrous inside; staminal column 4.5-7 cm. long, shorter to rarely equalling the petals, column irregularly dentate at the apex, filaments 2-4 mm. long, usually in pairs and arranged in 5 vertical rows; ovary sessile, ovate to conical, glabrous, 5-loculed, ovules about 5 in each locule; capsule ovoid, 3-5 cm. diameter, apparently fleshy when fresh becoming woody when dry, walls thick; seeds 3-5 in each locule, obovoid, 1.2-1.3 cm. long, 7-9 mm. broad, glabrous, black, cotyledons black dotted.

Illustrations: A. DC. Calq. Diss. Fl. Mex. Moc. & Sessé pl. 1. 1874.

PUERTO RICO: San German, at Lajas-arriba, *Sintenis 3957* (G, NY, US), in fruit in Sept.; Laguna Tortuguero, *Britton, Cowell & Brown 3835* (G, NY, US), in flower in Feb.; Vega Baja, *Stevens 1899* (NY), in fruit in Jan.; *Britton 8592* (NY), in flower in Feb.; Manatí, *Stevens 1955* (NY, US), in flower in June; Arecibo, *Hess & Stevens 5065* (NY), in fruit in Nov.; Río Nuevo, *Britton, Britton & Boynton, 8158* (NY), in flower in Jan.; Canovanas, *Holdridge 234* (NY), in flower in March; Bayamon, *Britton & Britton 3987* (NY), in flower in Mar.; *Britton, Britton & Boynton, 8454* (NY), in sterile condition in Mar.; *Sintenis 1050* (G, US, sheets labelled Type Collection), in flower in April; Pena de las Cuevas, near Juana Diaz, *Britton & Marble 2291* (NY, US), in flower in March; Yauco, *Sargent 594* (US), in flower in March; Dorada, *Miller 1616* (US), in flower in March. CUBA: Las Villas: Soledad, *Jack 8489* (NY), sterile condition in Feb.; *Howard 4114* (G), in flower in June. Both collections from cultivated material.

Local names: Maga, Magar, Magas (fide Urban).

The plants are native in Puerto Rico growing in woods and on hillsides away from the coast. The tree is commonly planted as a roadside tree for



FIGS. 1-6. *Montezuma grandiflora* (Holdridge 234). FIG. 1. Habit. Pubescence omitted; note fruiting pedicel after capsule has fallen. FIG. 2. View of glabrous seed. FIG. 3. Circumscissile calyx and young fruiting pedicel. FIG. 4. Longitudinal section of fruit. FIG. 5. Mature fruit. FIG. 6. Cross-section of mature fruit showing plump seeds in four locules. All drawings  $\times \frac{1}{2}$ .

shade or as an ornamental for its showy flowers. The wood is hard and durable and valued for furniture or for posts.

The collections of *Sintenis* 1050 (G, US) have been annotated "Type collection", by some earlier worker. The original description by DeCandolle refers to "*Hibiscus grandiflora* Juss. ined." and no specimens were cited. Since the *Sintenis* material is generally widely distributed, it seems proper to designate this collection as the type.

Urban established the genus *Maga* to accommodate *Thespesia grandiflora* DC. *Montezuma* Sessé & Moc. is an older name for the genus. Urban considered the circumscissile calyx which is deciduous, the glabrous seeds, a 3-4 locular ovary and the lack of black punctate dots in the cotyledons as generic characters. The first two, that is, circumscissile and deciduous calyx (figs. 1, 3), and glabrous seeds (fig. 2) may be maintained as generic characters. The ovary in all of the material I have examined has 5 locules in the flower but seeds may be developed in only 3 or 4 (fig. 6) of these or in all five locules. The cotyledons of the embryo do have black punctate dots although these are not as abundant as in species of *Thespesia*. Thus the latter two characters cannot be used to distinguish between *Montezuma* and *Thespesia*.

THESPESIA Soland.; Correa, Ann. Mus. Paris 9: 290. 1807. pl. 8, f. 2.

Shrubs or trees. Leaves alternate, entire, usually cordate or broadly 3-5-lobed; stipules linear. Flowers solitary and axillary on simple or jointed pedicels. Involucre of 3-15 bracteoles, these free, ovate, acute or acuminate, linear or filiform, persistent or caducous. Calyx subhemispheric, truncate or nearly so, persistent, expanding and becoming repand and undulate in fruit. Petals 5, united at the base. Staminal column shorter than the corolla, 5-toothed at the apex, filaments free from or united with the column. Ovary sessile, 5-celled, ovules 3 or 4 in each locule. Capsule woody or leathery, 3-5-celled, indehiscent. Seeds obovoid, compressed, pubescent, cotyledons black-punctate.

THESPESIA POPULNEA (L) Soland.; Correa, Ann. Mus. Paris 9: 290. 1807. *Hibiscus populneus* L. Sp. Pl. 694. 1753. *Malvaviscus populneus* Gaertn. Fruct. 2: 253. pl. 135. 1791.

Shrub or small tree 1-20 m. tall; young branches lepidote-stellate; stipules linear, 5-10 mm. long, early caducous; leaves ovate-orbicular to ovate-acuminate, 5-15 cm. long, 3-11 cm. broad, apex acuminate, base cordate, margin undulate, sparsely lepidote-stellate on both surfaces; palmately 5-nerved, occasionally with small domatia harboring scale insects in the axils; petioles 4-8 cm. long; flowers solitary, axillary, peduncles 2-4 cm. long; bracteoles 3, free, linear or acute, 1-1.4 cm. long, 2-3 mm. broad at the base, lepidote-stellate-pubescent; calyx subhemispheric, 1 cm. high, 1.5 cm. diameter, truncate or with 5 minute teeth, densely lepidote-stellate outside, pubescence inside the calyx of lepidote-stellate clusters with the free arms of the hairs to 4 mm. long, the pubescence appearing as tomentose; petals 4-7 cm. long, 3-5 cm. broad, yellow with a darker base changing in age to flesh color, orange, red or purple, numerous black punctate dots present at the apex of the petals and along the margins; staminal column 1.5-2 cm. long, shorter than the petals, sharply 5-toothed at the apex; ovary lepidote-stellate, 5-celled, ovules 4 or 5 at the base of each

locule; capsule depressed-globose, 3–4.5 cm. diameter, 1.5–2 cm. high, leathery, indehiscent, fruiting calyx repand, often strongly undulate, 2 cm. in diameter; seeds usually 3 in each locule, obovoid, compressed and flattened on 2 surfaces, densely tomentose-stellate, often long-bearded at the base, secondary crispse pubescence often developed.

Common tree in coastal woods and edges of mangrove swamps or along sea coast on sandy soil. Widely planted in the tropics as a shade or ornamental tree. Flowers commonly eaten as food. Fruit used medicinally for treatment of skin eruptions.

BERMUDA: Holly Lodge, *Brown & Britton 1611* (NY, US), cultivated. BAHAMAS: New Providence; Hog Island, *Wilson 8321* (NY) in sterile condition in June; *Britton & Mulsbaugh 2176*, in sterile condition in Jan.; Nassau, *Curtis 173* (G, NY, US); Grants-town, *Wilson 8221*, (NY); Inagua, Mathew town, *Nash & Taylor 1473* (NY), cultivated; Turks Islands: Grand Turk, *Nash & Taylor 3840* (NY). CUBA: Havana: Playa del Rincon de Guanabo *Leon, Sanchez & Cubas 8493* (NY); Playa de Baracoa, *Leon 8422* (NY); Las Villas: Calicita, *Combs 522* (G, NY, US); Bahia de Cochinos, *Roig & Cremata 2167* (US); Punta Diablo, Cienfuegos Bay, *Britton & Wilson 6043* (NY); Soledad, *Howard 4176* (G), *Jack 4056* (US), *5347* (US), cultivated. Matanzas, Valley of the Yumuni, *Britton, Britton & Shafer 211* (NY); Oriente: Santiago, *Pastor 1811* (NY); Santiago Bay, *Sedro & Leon 3951* (NY); Gibara, *Shafer 1511* (NY, US); Santiago, *Underwood & Earle 1660* (NY); Las Minas, P. Principe, *Wright 1576* (G). JAMAICA: Bowden, *Britton 4017* (NY); Folly Point, *Fredholm 3166* (NY, US); Kingston, *Brown 356* (NY, US); Montego Bay, *Maxon & Killip 1623* (G); Roekport, *Killip 23* (US); Mandeville, *Miller 1406* (US); Hunts Bay, *Maxon & Killip, 326* (US). HAITI: Tortue Island, Basse Terre, *Leonard & Leonard 13919*, (G, NY, US); La Vallee, *Leonard & Leonard 15350*, (NY, US); Miragoane near Carenage, *Ekman 8578* (US); Miragoane, *Eyerdam 166* (G, US); Port-au-Prince, *Holdridge 1228* (NY, US). PUERTO RICO: Coamo, *Goll, Cook & Collins 751* (NY); Ponce, *Underwood & Griggs, 729* (NY, US); Fajando, *Heller 818* (US, NY), *Sintenis 1135* (US), *Evermann 1238* (US), *1246* (US); Parguera, *Sargent 452* (US); Vieques Island, Isabel Segunda, *Shafer 2392* (NY, US). ST. THOMAS: *Eggers 389* (G). ST. CROIX: Golden Rock, *Ricksecker 197* (NY, US); *Thompson 1056* (G); *Britton & Cowell 23* (NY). GUADELOUPE: *St. Rose 2779* (NY, US); Vieux-Fort, *Stehle 101* (NY). MARTINIQUE: *Galian, Duss 2024* (NY). ST. BARTS: *Gustavia, Questel, 123* (NY). ANTIGUA: St. Georges, *Box 1040* (US). MONTSEERAT: Plymouth, *Shafer 101* (NY, US). DOMINICA: Prince Rupert Bay, *Hodge 544* (NY, US); Pointe Ronde, *Hodge 2693* (G). GRENADA: Grand Anse, *Broadway S.N.* (NY, US); St. Georges, *Broadway S.N.* (NY, US). GRENADINES: *Beequia, Joseph B-160* (NY). TOBAGO: The Bay at Scarborough, *Broadway 4383* (G, US).

The specimens cited above were collected in flower or fruit in every month but June.

Specimens have also been examined from Florida, Panama, British Honduras, Colombia, Venezuela, British Guiana, Brazil, and Australia.

Local names: Cork-tree, Spanish Cork, Emajaguilla, Palo de Jaqueca, Santa Maria, Bendy-tree, Otaheite, Clamor (Puerto Rico); Álamo Hiquillo, Majagua de la florida (Cuba); Gros Mahaut (Haiti); Álamo, Álamo blanco (Dominican Republic); Catappa (Guadeloupe); Seaside Mahoe (Florida).

ULBRICHIA Urb. Dansk. Bot. Arkiv. 4: 7–8. 1924.

*Armouria* Lewton, Jour. Wash. Acad. 23: 63–64. 1933.

Shrubs or trees, leaves alternate, petiolate, strongly angular-lobed, stipules linear, deciduous. Flowers solitary, axillary, on simple peduncles. Involucre of 3 linear to linear-lanceolate bracteoles, persistent or deciduous.

Calyx cyathiform, truncate to minutely 5-toothed, substipitate at the base. Petals 5, united at the base. Staminal column shorter than the corolla, 5-toothed at the apex. Ovary sessile, 5-celled, ovules 4-5 in each locule; stigmas and styles united. Capsule conical to ovoid, loculicidally 5-valved at the apex, densely lepidote-stellate-pubescent. Seeds obovoid, black, glabrous and shining, cotyledons black-dotted.

ULBRICHIA BEATENSIS Urb. Dansk. Bot. Ark. 4: 8. 1924. *Armouria beata* Lewton, Jour. Wash. Acad. 23: 64. 1933. *Thespesia beata* Hutchin. New Phytol. 46: 136. 1947.

Shrub or tree to 8 m. tall; young branches lepidote-stellate; stipules linear, 5-6 mm. long; leaves orbicular in outline, the very young ones cordate-ovate, the older leaves 3-5-angled or lobed, 3-6 cm. long, 3.5-7 cm. broad, apex obtuse, base deeply cordate, the lobes overlapping, margin entire, lepidote-pubescent above, soft-lepidote-tomentose below, palmately 7-9-nerved, the midvein with a linear gland midway between base and apex; petioles 1-7 cm. long, peduncles 3-5 cm. long, slightly thickened below the calyx, bracteoles 3, linear-lanceolate, 3-4 mm. long, deflexed; calyx cyathiform 1.2 cm. long, 1.5 cm. diameter becoming 1.5 cm. long and 2.5 cm. diameter in fruit, densely and minutely lepidote outside, densely sericeous inside, truncate or minutely 5-toothed at the apex, constricted into a short stipe at the base; petals 5-6 cm. long, 3.5 cm. broad, cream-colored or white, black-dotted and lined in the middle, wooly-tomentose outside when young, glabrous inside; staminal column 3.5 cm. long, shorter than the petals, with 5 linear-lanceolate teeth at the apex; filaments 2.3 mm. long; ovary 5-celled, ovules 1.3-1.5 mm. long, densely lepidote-stellate-pubescent, capsule short-globose, 1.5-2 cm. long, 1.8-2.3 cm. diameter, apex abruptly and narrowly acuminate, the acumen 5 mm. long, densely lepidote-stellate pubescent, half enclosed in the calyx, loculicidally 5-valved at the apex; seeds obovoid, 7.5-11 mm. long, 5 mm. broad, 4.5 mm. thick, black, cotyledons black-resinous-dotted.

DOMINICAN REPUBLIC: Island of Beata, northern end, *Ostenfeld 312* (type not seen), flower in Feb.; rocky cliff near middle of west side of island, *Fairchild and Dorsett 2617* (US 1, 555, 481, TYPE of *Armouria beata*, duplicates and photographs), in flower and fruit in Jan. FLORIDA: U.S.D.A. Plant Introduction Garden, Coral Gables, *Loomis s.n.* (NY-sterile).

Illustration: Dansk. Bot. Ark. 4: pl. 1. 1924.

The publication by Urban of *Ulbrichia* in a relatively obscure Danish publication has caused the genus to be overlooked by all recent students of the Malvaceae. *Ulbrichia beatensis* Urb. antedates *Armouria beata* Lewton and must replace the latter name. Both specimens were collected from Beata Island off the southern coast of the Barahona peninsula of the Dominican Republic.

Mr. Harold Loomis, director of the Plant Introduction Garden of the U. S. Dept. of Agriculture at Coconut Grove, Florida, was one of the botanists on the Fairchild-Dorsett expedition which found the plant described as *Armouria*. Mr. Loomis recognized the horticultural possibilities of this plant and brought back seeds from the type plant which have been grown at the Plant Introduction Garden. It was my pleasure to see the progeny of the type plant in flower at Coconut Grove in June of this year. The

handsome flowers are cream-colored and 4-5 inches in diameter. Unfortunately this tree has not set viable seeds. In discussing this collection Mr. Loomis told me only one group of these plants was found on Beata Island and it seems probable that the specimen described by Urban was taken earlier from the same plant as the Fairchild-Dorsett specimen.

A request has been made to the Bureau of Plant Industry that specimens be made of this interesting plant and that they be distributed to the various herbaria of the world. In the U. S. National Herbarium there are three sheets of photographs taken by Mr. Loomis of flowers and fruits of the specimen growing at Coconut Grove.

### *Atkinsia* Howard, gen. nov.

Floris in spicis terminalibus aphyllis, calyce lignoso, persistenti, staminum columna corollam excedenti, capsula indehiscenti, seminibus glabris.

Trees. Branches and leaves densely covered with a lepidote or lepidote-stellate pubescence at least when young. Leaves alternate, petiolate; stipules not seen. Flowers solitary on stout peduncles in terminal leafless short spikes, flowering spikes with minute terminal buds often developing next year's growth. Involucre of 3 linear-lanceolate bracteoles, deciduous or persistent becoming contorted, falcate and woody in fruit. Calyx persistent, campanulate, truncate at the apex with 5 linear teeth, or variously lobed. Petals 5, imbricate, densely lepidote-stellate outside at the base, lepidote-scurfy outside above, glabrous inside. Staminal column longer than the corolla, filaments fused in pairs, anthers divaricate, strongly hippocrateriform. Styles united, stigmas clavate. Ovary lepidote-pubescent, 5 (3)-celled. Capsule indehiscient, globose, apiculate, 1-3-celled with remnants of the others; seeds 1-3 in each cell, black, glabrous; cotyledons folded, black-punctate. Fruiting calyx woody, irregularly split, investing the fruit.

TYPE SPECIES: *Maga cubensis* Brit. & Wils.

*Atkinsia cubensis* (Brit. & Wils.) Howard, comb. nov. (figs. 7-14). *Maga cubensis* Brit. & Wils. Mem. Torrey Club 16: 81. 1920. *Montezuma cubensis* Urb. Repert Sp. Nov. 18: 117. 1922. *Thespesia cubensis* Hutchin. New Phytol. 46: 135. 1947.

Tree to 17 m. tall; branches stout, densely lepidote-pubescent, lenticels round, conspicuous; leaves ovate-orbicular to ovate-cordate, 6-10 cm. long, 7-13 cm. broad, apex acute or acuminate, base deeply cordate or rarely subtruncate, coriaceous, margin entire, densely lepidote-stellate on both surfaces becoming glabrate, palmately 5-7-nerved at the base, midvein with linear gland about the middle of its length, the nerves connected at the base on lower surface by a membranaceous web forming domatia for scale insects; petioles 4-7.5 (10) cm. long; stipules not seen; flowers solitary on stout peduncles 2-6 cm. long, 5-7 clustered on leafless terminal shortened shoots; bracteoles 3, linear-lanceolate, 7-9 mm. long, caducous or persistent becoming woody and contorted; calyx campanulate, 9-12 mm. long, 1-1.7 cm. diameter, truncate with linear-subulate teeth to 3 mm. long or variously ruptured by the expanding bud, densely lepidote-stellate outside, densely lepidote-stellate or tomentose inside; petals 5, 3 cm. long, 1.3-1.5 cm. broad, yellow-white to yellow-brown becoming darker with age, black dots arranged in rows along the veins; staminal column 5-6 cm. long, twice as long as the corolla, filaments usually fused in pairs, 2 mm. long; ovary 3-5-celled, ovules 1-3 in each



FIGS. 7-14. *Atkinsia cubensis* (Jack 4959). FIG. 7. Habit showing leafless cluster of flowers and persistent woody calyx. Pubescence omitted. FIG. 8. Bud. FIG. 9. Cross section of fruit with two fertile locules. FIG. 10. Cross section of seed showing black punctate cotyledons. FIG. 11. Longitudinal section of seed. FIG. 12. Side view of seed. FIG. 13. Lower surface of leaf blade showing axillary webs and scale insect domatia. FIG. 14. Flower showing staminal column exceeding the corolla. All drawings  $\times \frac{1}{2}$ .

locule; capsule depressed-globular, apiculate, 2.5 cm. long, 3 cm. diameter, fleshy, becoming woody, the inner portion of the wall heavily filled with black resinous material, surface sparsely lepidote; seeds obovoid or rounded, flattened on 1-2 sides, 8-13 mm. long, 7-8 mm. broad, 4.5-7 mm. thick, glabrous.

CUBA: Las Villas: Caunao River, *Jack 4959* (NY, US), *Jack 5010* (NY, US), in flower and fruit March; Caunao River at Iguana Point, *Jack 5132* (NY, US), in fruit in April; Guabiro, near Soledad, *Jack 6955* (US), in flower in March; Cienfuegos Bay, Punta Diablo, *Britton & Wilson 6045* (NY, Type and two isotypes), in flower in March; Rineon to Banao, *Shafer 12175* (NY, US), in flower in Feb., *Shafer 12311* (NY), in fruit in March. Camaguey: La Gloria to Pilota, *Shafer 566* (G, NY), sterile in Feb. Oriente: Papayo of the Sevilla tract, Mandingo hill, *Ekman 9444* (NY), at 700 m. alt., sterile in Aug.; San German, *Ekman 6355* (NY), sterile in Aug.; Rio Cauto at Central Cauto, *Ekman 16124* (NY, US), in flower in Jan.

Urban (Repert. Sp. Nov. **24**: 237. 1928) also cites two Ekman collections from Pinar del Rio which I have not seen, *Ekman 17667* collected between Chambergro and Charco del Toro, and *Ekman 12867*, collected near Mariel and Tinaya.

Local names: Negra cuba, Majagua de Cuba (fide Ekman), Majagua peluda (fide Urban), Majagua negra (fide Leon).

The original description of *Atkinsia cubensis* by Britton and Wilson, under the generic name of *Maga*, is sketchy. Urban elaborated and corrected this description citing additional material collected by Ekman (Repert. Sp. Nov. **24**: 237. 1928).

Britton and Wilson described the calyx as circumscissile. I have examined the type and two isotype specimens as well as the additional material cited above and find the report of this character to be entirely an error. The fruiting calyx of *Atkinsia cubensis* is woody and enlarged but still encloses the depressed capsular fruit (fig. 7). During the enlargement the fruiting calyx is ruptured and the sections are irregular. They persist on the fruiting peduncle after the capsule falls (fig. 7). The fruiting peduncles finally break free from the branch or the main axis with the calyx still intact. It was on the supposedly circumscissile calyx that Britton and Wilson assigned this species to *Maga* Urb., and Hutchinson still uses this erroneous character to separate this species in his treatment of *Thespesia*.

The nerves of the cordate leaf are stout and palmately arranged in *A. cubensis*. On the lower leaf surface the nerves are joined at the base by a membranaceous web forming small cavities. In many cases these cavities are filled with scale insects and might properly be called domatia. Whether or not the insects are present, the membranaceous webs are always present and characterize this genus and species. The webs frequently extend to a point between the nerves and often show signs of a strong vascular ridge or fold extending into the web and into the point.

Hutchinson describes the leaves of *A. cubensis* as being "very deeply cordate or auriculate, the auricles often overlapping." Such a condition does not exist in the material I have seen. The leaf base is slightly cordate and the auricles never overlap.

The inflorescence is described by Hutchinson as sympodial. Actually 5-7 flowers may be produced at the apex of a stout branch. In flowering condition this axis is without leaves but very young leaves have been observed in



some specimens after the fruits have fallen. The following year's growth is often produced through a terminal bud on this floral axis. Older specimens of several years' growth will show this region of flower production appearing almost as a short shoot condition.

The ovary is 5-celled in most of the flowers I have examined. In fruit, however, usually only 3-4 locules will be fully developed with plump seeds.

The genus *Atkinsia* is named in honor of the Atkins family, especially Katherine Atkins and the late Edwin Atkins, who have done so much for the study of botany and of tropical botanical problems through the establishment of the Atkins Garden and Research Laboratory of Harvard University at Soledad, near Cienfuegos, Cuba.

THE NEW YORK BOTANICAL GARDEN  
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# THE MORPHOLOGY OF CHLAMYDOMONAS CHLAMYDOGAMA, SP. NOV.

HAROLD C. BOLD

During the past three years while engaged in studying clonal cultures of *Chlamydomonas* from soil samples, with the ultimate purpose of obtaining data for comparison with those obtained by Moewus (1938a,b, 1939a,b,c, 1940a,b,c, 1943), the writer isolated an interesting form from a Venezuelan soil sample.<sup>1</sup> The ease with which the organism can be maintained in culture, as well as its readily demonstrable sexuality impel the writer to describe its morphology, and to make it available for demonstration and further study by others.

As noted by Smith (1946) in his brief summary of some aspects of Moewus' work, the certain identification of species of *Chlamydomonas* and related organisms is fraught with difficulties. Many specific descriptions are markedly incomplete, unsupported by prolonged critical observations, cultural studies, and adequate illustrations. Furthermore, the herbarium specimens available usually do not reveal the morphological details on the basis of which species are distinguished. Finally, the nature of the zygospore and its behavior upon germination have been recorded for relatively few species.

The present organism (figs. 1-21) belongs obviously in the subgenus *Agloë* (Pascher 1927, Gerloff 1940) of the genus *Chlamydomonas*, and is in some respects most similar to *C. sylvicola*, a form incompletely described by Chodat (1921). Although a number of species of *Chlamydomonas* possess walled gametes, this feature is so marked and readily observable in the present organism that the latter will be described as:

***Chlamydomonas chlamydogama* Bold, sp. nov.** Cellulae e 13.2 ad 26.4  $\mu$  longitudine, e 5.0 ad 9.0  $\mu$  latitudine, ellipsoidales vel cylindroidales, saepe quomodo reniformes. Muri cellulares frequenter separati ab protoplastis in parte posteriore. Cellulae sine papilla; vacuoles contractiles gemini, anteriores. Stigma instans, in parte anteriore. Chromatophora velut H, cum pyrenoide unico axiale. Nucleus posterior. Propagatio asexualis per 2 vel 4 cellulas intra cellulae maternae membranam ortas. Propagatio sexualis heterothallica et isogamica; zygotes non rubri, semper virides, cum membranis unornatis, quadrifariam germinantes. Hab.: In solum Venezueliensem.

<sup>1</sup> The writer is indebted to Dr. Kenneth B. Raper, Northern Regional Research Laboratory, U.S.D.A., for making foreign soil samples available.

**Material and Methods.** Air dry soil of sample W-16 (from Venezuela) was introduced into Erlenmeyer flasks containing 100 ml. of modified sterile Bristol's solution (Bold 1942). The solution is prepared as follows: six stock solutions, 400 ml. in volume are employed, each containing one of the following salts in the concentration listed:

NaNO <sub>3</sub>	10.0 grams	KH <sub>2</sub> PO <sub>4</sub>	7.0 grams
CaCl <sub>2</sub>	1.0 gram	MgSO <sub>4</sub>	3.0 grams
K <sub>2</sub> HPO <sub>4</sub>	3.0 grams	NaCl	1.0 gram

10 ml. of each stock solution are added to 940.0 ml. of Pyrex-distilled water. To this are also added one drop of a 1.0 per cent FeCl<sub>3</sub> solution and 2 ml. of minor elements solution (Craig & Trelease 1937).

The cultures were illuminated in an artificial cooled light (Bold 1936) or by fluorescent light of approximately 50 foot-candles intensity. Within two weeks after setting up the cultures a delicate, green, positively phototactic ring of motile algae appeared in the flasks, from which individual *Chlamydomonas* cells were isolated with micropipettes. The organisms may be maintained also in Knop's solution as prepared by Moewus (1940b), and on solid media in which either Bristol's or Knop's solutions have been compounded with 1.5 per cent agar. The cells are nonmotile on agar, but remain motile in liquid cultures with adequate nutriment and illumination. Microscopic study over prolonged periods was most successful in hanging-drop preparations.

**Observations.** The specific description given previously is based on several years' observation of clonal cultures isolated from soil. The variations in cell size probably represent cells in various stages of development after their liberation from parent cells at the conclusion of cell division. The cell wall lacks a papilla, but two small flagellar orifices are apparent (fig. 18) when the protoplast contracts during cell division. Mature cells frequently have their protoplasts markedly withdrawn from the posterior portion of the wall (figs. 2, 4, 5). Study of cells stained with methylene blue indicates that this contraction is not induced by a thickening of the basal portion of the wall, but rather that an autonomous withdrawal of the protoplast occurs. The latter may also be slightly withdrawn from the anterior portion of the wall (figs. 1, 2, 4, 5), and in some cases forms a papilla-like beak (fig. 5). The flagella are approximately of body length.

Although somewhat variable, the chloroplastid in median, longitudinal, optical section (figs. 1, 2) exhibits the "H"-shaped structure characteristic of members of the subgenus *Agloë*. The posterior and anterior openings are frequently small, with the prominent single pyrenoid lying in the central bridge of the chloroplastid. Two contractile vacuoles, which function alternately, occupy the anterior portion of the protoplast (figs. 1, 2, 5), and, as

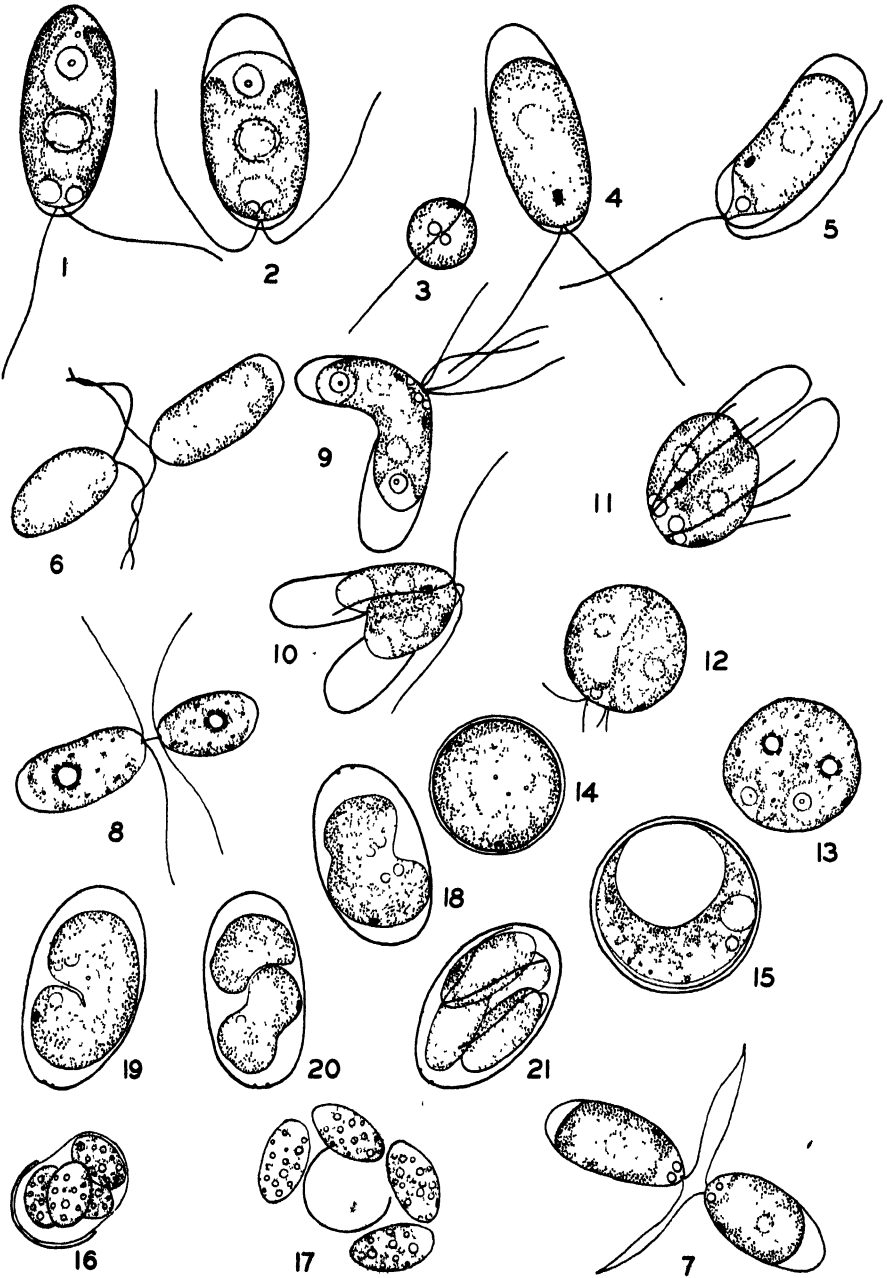
is usual in the genus, lie in a plane perpendicular to that occupied by the flagella (fig. 3). The stigma, which varies considerably in size and form, is embedded in the anterior third of the chloroplastid (figs. 1-5). As in many species of the subgenus *Agloë*, the nucleus lies in the posterior, colorless cytoplasm (figs. 1, 2, 9).

In thriving cultures cell division occurs most abundantly at night if the cultures are darkened. The products of division are usually liberated during the following morning. Cell division occurs only in nonmotile cells whose flagella have been withdrawn (fig. 18). Owing to a rotation of the protoplast within the wall the first cleavage appears transverse (fig. 19). The cells figured as 18 and 19 indicate that a duplication of contractile vacuoles occurs before cytokinesis. No evidence for their origin by division has been observed. As a rule each dividing cell undergoes one or two successive bipartitions so that the daughter cells are two or four in number (fig. 21). Immediately after division only one of the division products contains a stigma, presumably that of the parent cell (fig. 21), but subsequent to liberation a small stigma appears in each of the others. The daughter cells become flagellated in the early morning and become feebly motile; the surrounding mother wall is ruptured by the violent activity of the daughter cells.

Like *Chlamydomonas eugametos* Moewus, the gametes of *C. chlamydogama* are morphologically indistinguishable from vegetative cells. However, their slightly but constant smaller size (figs. 6-11) indicates that they are recently divided cells. *C. chlamydogama* is strictly heterothallic, no evidence of sexuality having been observed in several years' study of individual (segregated) clonal cultures. Of the six clones originally isolated, two were apparently of one sex and four of the other, as determined by their mating reactions. The gametes of *C. chlamydogama* are fundamentally isogamous; although gametes of unlike size frequently fuse, just as frequently two large and two small gametes may be observed uniting.

The sexual process occurs regularly when cells from clonal cultures of unlike sex are mixed together in hanging-drop preparations, in which the details of the process may be readily followed (figs. 6-15). The writer's observations indicate that the speed, intensity (as evidenced by degree of clumping), and duration of the sexual process vary with such factors as the age of the cultures, the concentration of the gametes, and others, all of which will comprise the subject of a subsequent contribution. Unlike Moewus' *C. eugametos* (1938a), the cells of *C. chlamydogama* remain motile during prolonged periods of darkness, but copulation of gametes occurs only in illuminated cultures.

The sexual process from the time the gametes first approach (fig. 6) until the complete withdrawal of the flagella by the zygote (fig. 13) occupies



between  $1\frac{1}{2}$  and 2 hours. If hanging-drop preparations are examined immediately after the clones are mixed, a rather marked decrease in motility is apparent, but within five minutes active motility recurs. Certain of the cells become anchored to the coverglass by their flagellar extremities, and exhibit rather violent, jerky movements. Others, which have been free-swimming, aggregate around the nonambulatory cells forming more or less extensive groups in which individual pairs are formed, at first by entanglement of flagella (fig. 6), but almost immediately the flagella appear to agglutinate at their tips (fig. 7). Such pairs move by jerky movements, and never far from the point of original union, apparently because the flagellar tips are rather firmly attached to the substratum. No evidence for negative phototactic reactions of fusing gametes is apparent in hanging-drop cultures. The cells continue in this condition (fig. 7) often for more than an hour, undergoing violent but localized movements during which the anterior poles of the cells are vigorously brought together. The rupture of the cell wall of each gamete is achieved probably through both mechanical and chemical means. Evidence of the latter is available in the examination of cast-off gamete walls which usually have a frayed, hydrolyzed appearance at their anterior portion.

The first permanent union of the protoplasts occurs in the region of their blepharoplasts, and at the moment of union, the flagella, which have been actively motile while still terminally united, separate entirely from each other (fig. 8), and subsequently carry on only very feeble motion. Careful observation indicates that frequently at this stage the mating gametes are connected by a protoplasmic thread (fig. 8), also observed by

#### Explanation of figures 1-21

All figures were drawn with the aid of a Leitz camera lucida, and reduced  $\frac{1}{2}$  in reproduction. The approximate magnification is 1553, except figures 16, 17, for which it is 700. All are from living material except where indicated in the legends.

FIG. 1. Vegetative cell in median longitudinal optical section (m.l.o.s.); protoplast in contact with posterior portion of wall. FIG. 2. Vegetative cell in m.l.o.s., protoplast contracted posteriorly. FIG. 3. Anterior polar view of vegetative cell. FIG. 4. Vegetative cell in surface view. FIG. 5. Slightly reniform type of vegetative cell, protoplast beak-like anteriorly. FIGS. 6-15. Sexual reproduction. FIG. 6. Initial entanglement of flagella. FIG. 7. Terminal agglutination of flagella. FIG. 8. Gametes stained with IKI solution, protoplasmic thread apparent between blepharoplasts. FIG. 9. Early stage in protoplast fusion. FIG. 10. Gamete protoplasts escaping from walls. FIG. 11. Later stage, gamete protoplasts almost entirely shed. FIG. 12. Still later stage, gamete protoplasts still delimited, flagella disappearing. FIG. 13. Zygote stained with IKI solution. FIG. 14. Zygospore with wall, 48 hours after union, one pyrenoid is markedly smaller, stigmata still visible. FIG. 15. Zygospore 1 week after union of gametes; large vacuole-like and smaller oil droplets visible. FIG. 16. Germination of the zygospore on Bristol's agar medium. FIG. 17. Liberation of products of zygospore germination on Bristol's agar. FIGS. 18-21. Asexual reproduction, cell division. FIG. 18. Rotation and first cleavage of protoplast; note duplication of contractile vacuoles, but not stigma. FIG. 19. Stage similar to 18, but cleavage unilateral. FIG. 20. Early stage in second cleavage. FIG. 21. Four daughter cells, flagellated, just before liberation.

Strehlow (1929) in *Polytoma uvella*. Once their contact has become established, union of the gamete protoplasts (figs. 9–13) proceeds with great rapidity: they flow out of the cell walls, and fuse completely leaving the empty gamete walls behind. The flagella become shortened and attenuated, and finally disappear (fig. 13). Observation of living cells indicates that they are withdrawn, although it is possible that this appearance is due to acropetal hydrolysis. The individual gamete protoplasts are recognizable within the zygote often for as long as 24 hours after fusion, as are also their contractile vacuoles, pyrenoids, and stigmata. The exact time of nuclear fusion has not yet been determined. After 48 hours, however, the individual gamete protoplasts are no longer recognizable, a wall is secreted around the zygote (fig. 14), and one of the gamete pyrenoids ultimately disappears. The zygospore then enlarges considerably (fig. 15), and, if retained in the same culture medium in which fusion occurred, loses some of its chlorophyll and develops droplets of colorless oil.

Zygospore germination has been obtained by transferring zygospores a week after their formation from the hanging-drop preparations to the surface of nutrient agar. The first germinations occurred within 48 hours. In every case observed the contents of the zygospore underwent two successive bipartitions resulting in the liberation of four daughter protoplasts (figs. 16, 17). These became motile when flooded with liquid nutrient solution.

**Discussion.** In spite of implied criticism (Philip & Haldane 1939) of Moewus' numerous contributions dealing with sexuality in *Chlamydomonas* and other organisms, one can not avoid being impressed and stimulated by the importance of the fundamental problems they involve. Smith (1946) has expressed a similar view, and has reviewed some of the more important aspects of Moewus' work, which have no direct bearing here. A complete and final confirmation of Moewus' results can be effected only by using precisely the same organisms which the latter studied, but significant comparative data will certainly be obtained by studies of sexuality in other species.

The observations reported in this paper are preliminary in that they are entirely morphological; further work on other aspects is in progress. However, although sexual union in *Chlamydomonas* species has been reported again and again, the more detailed phases of the process have often been omitted. The ease with which *C. chlamydogama* may be cultivated as well as its ready manifestation of sexuality suggest to the writer that it should be made available both for instructional and research purposes.<sup>2</sup>

<sup>2</sup> Unialgal cultures of the heterothallic strains W16-1 and W16-2 of *C. chlamydogama* will be sent at the request of anyone desiring them for purposes of teaching and research. The cultures are maintained in the modified Bristol's solution described in the text. It is regretted that it will be necessary to request a fee of one dollar to cover costs of mailing and maintenance of cultures by a laboratory technician.

From a morphological viewpoint several of the observations reported herein are of interest. One is inclined to infer that those gametes which first become attached by their flagella to the substratum, and which subsequently unite with more actively motile individuals, are female. There is some similarity here with Hartmann's (1934) description of sexuality in *Ectocarpus siliculosus*. More convincing proof of the female nature of the less active gametes of *C. chlamydogama* would be their regular preference for the male gametes of a heterogamous species.

Although many accounts of gamete union in the algae emphasize the importance of flagellar entanglement in effecting fusion, it certainly plays a minor role in *C. chlamydogama*; the entanglement here is only momentary, and is followed immediately by what appears as a terminal agglutination effected chemically. This condition persists for an hour or more, and the evidence indicates that during this period dissolution of the gamete walls is achieved both mechanically and by the mutual secretion of some hydrolysing agent. Experimental evidence for the chemotactic nature of gamete union has been reported by Moewus (1939b). The union of the gamete protoplasts themselves is fundamentally similar to the same process in Zygnematalean genera like *Closterium*.

#### SUMMARY

1. A specific diagnosis of an undescribed species of *Chlamydomonas*, *C. chlamydogama*, is presented.
2. The organism was originally isolated from a soil sample from Venezuela, and clonal cultures may be readily maintained in Bristol's, Knop's, and probably other media.
3. The morphology of the organism is described and illustrated.
4. *C. chlamydogama* is strictly heterothallic; sexuality is readily manifested when organisms from clonal cultures of different sex are brought together in hanging-drop preparations.

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VARIATION IN A NATURAL POPULATION OF  
*PLANTAGO ARISTATA*

RICHARD H. GOODWIN

The extreme variability of the little plantain, *Plantago aristata* Michx., first attracted my attention while I was making a survey of the flora of Mendon Ponds Park, Monroe County, New York (Goodwin 1943). This species was found growing in profusion in and beside a bridle path which runs along the sandy crest of an esker. Collections were made in 1941 and 1942 at this station.

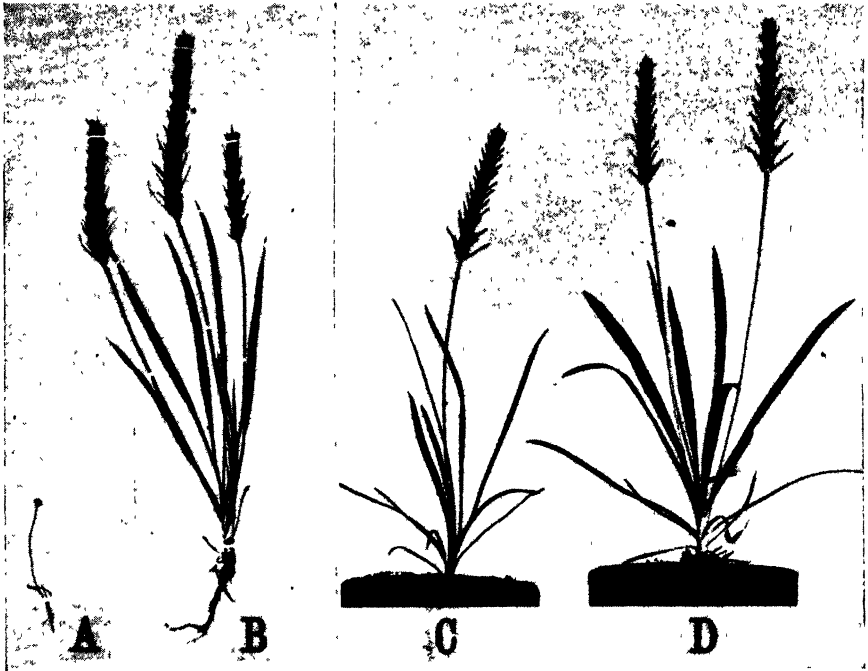
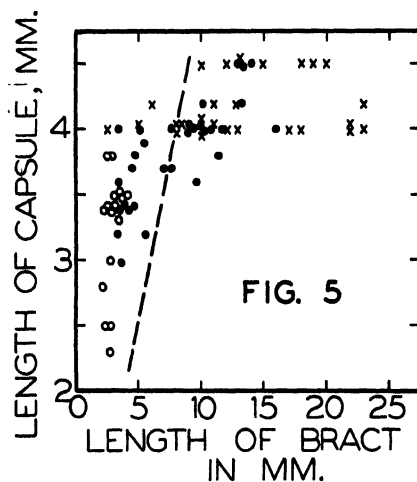
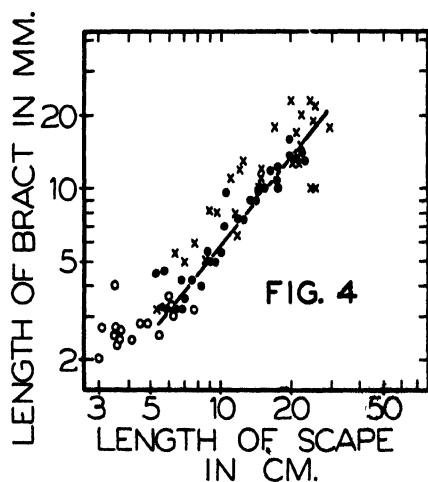
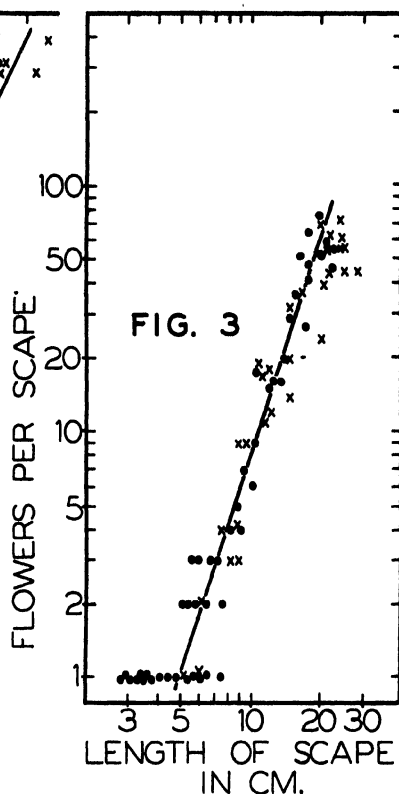
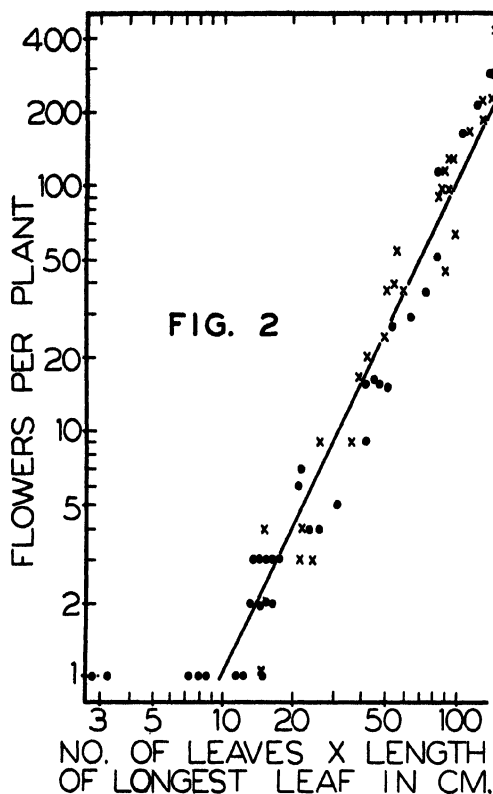


FIG. 1. Photographs of *P. aristata*.  $\times \frac{1}{2}$ . A. Depauperate, one-flowered specimen from Mendon. B. Large, vigorous specimen from Mendon. C, D. Plants grown in greenhouse from seeds of specimens similar to those shown in figures 1A and 1B, respectively.

*P. aristata* is a midsummer-flowering annual with a basal rosette of linear leaves and one or more flowering scapes. The smallest plants collected had solitary, one-flowered scapes about 3 cm. long and two thread-like leaves about 1.5 cm. long (figure 1A); the largest had as many as seven scapes over 20 cm. long with up to 76 flowers per scape and with as many as 13 leaves



up to 13 cm. in length. A large plant is shown in figure 1B. All plants collected had reached maturity; that is, the capsule contained mature seeds. Some of the largest plants still had some immature flowering scapes, but only the fully-developed ones were measured. The following measurements were made; number of leaves and length of the longest leaf; number and length of the scapes; number of flowers per scape; length of the capsule (from the base to the point of reflection of the corolla lobes); length of the seed; and length of the lowest bract of the inflorescence.

Similar data were also obtained from the following specimens from New York in the Cornell University Herbarium: Flushing, Long Island, July 15, 1936, *J. Monackino* 93; Islip, Suffolk County, Long Island, June 24, 1925, *W. C. Muenscher* 16291; Lake Ronkonkoma, Long Island, August 17, 1938, *Muenscher & Curtis* 6497; Waneta Lake, Schuyler County, July 11, 1934, *R. T. Clausen* 1389; Ithaca, August 1, 1904, *E. M. Cipperly*, September, 1903, *F. W. Foxworthy*.

The first relationship to be presented is one between vegetative vigor and the extent of reproduction. If we assume that there is a direct relationship between these two phases of development, then the total number of flowers per plant, which is a measure of the amount of reproductive material produced, might be expected to increase as a function of the quantity of the photosynthetic tissue; however, in this study the product of the number of leaves per plant times the length of the longest leaf has been used as an index of vegetative vigor. Figure 2 shows the relationship between total number of flowers and the leaf length index plotted on a double logarithmic grid. With the exception of the smallest, one-flowered plants, all the plants measured fall nicely along a straight line which has a slope of 2 and which satisfies the mathematical expression:  $y = bx^2$ , where  $b$  is a constant with a value of  $10^{-4}$ . This shows that reproduction in these plants is a definite function of their vegetative vigor. The exact significance of the value  $x^2$  is not certain, but it may not be too bad an approximation of the amount of photosynthetic tissue. If this were true,

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FIG. 2. Total number of flowers per plant ( $y$ ) plotted on a double logarithmic grid against the product of the number of leaves per plant and length of the longest leaf ( $x$ ). The line represents the formula  $y = 10^{-4}x^2$ . It is a close, but not necessarily best, fit for the data. Dots: data for Mendon specimens. Crosses: data for other New York collections. FIG. 3. Number of flowers per scape ( $y$ ) plotted against length of scape ( $x$ ) on a double logarithmic grid. The line represents the expression  $y = bx^3$ , where  $b$  is a constant with a value  $8 \times 10^{-6}$ . This relation becomes a straight line with a slope of 3 when plotted logarithmically ( $\log y = \log b + 3 \log x$ ). Symbols as in figure 2. FIG. 4. Length of lowest bract ( $x$ ) plotted against length of scape ( $y$ ) on a double logarithmic grid. Open circles: Mendon specimens with one flower only. Dots: Mendon specimens with two or more flowers. Crosses: data for other New York collections. FIG. 5. Length of capsule plotted against length of lowest bract. The ratio: length of bract/length of capsule, is less than 2 for all plots falling to the left of the broken line. Symbols as in figure 4.

their reproduction would appear to be directly proportional to their photosynthetic capacity.

Within the inflorescence, there is a close and direct relationship between the length of scape and the number of flowers produced thereon. Figure 3 shows the data plotted on a double logarithmic grid. With the exception of the smallest of the one-flowered plants, the plots fall along a straight line which has a slope of 3. The formula expressing this relationship is  $y_0 = bx_0^3$ , where  $y_0$  equals the number of flowers,  $x_0$  equals the length of the scape in mm., and  $b$  is a constant. Since  $y_0$  essentially represents a volume, and  $x_0$  a linear dimension, raising  $x_0$  to the third power should make the two sets of measurements comparable.

The formula of heterogonic growth (Huxley 1932) is  $y = bx^k$ , where  $y$  is the size of a particular structure,  $x$  is the size of the whole organism,  $k$  is the ratio of the growth rate of  $y$  to the growth rate of  $x$ , and  $b$  is a constant. Applying this to the scape and inflorescence,  $y = y_0$ ,  $x = x_0^3$ ,  $b = 8 \times 10^{-6}$ , and  $k = 1$ . This value of  $k$  may be interpreted as indicating that inflorescence and scape have the same relative rates of growth.

The relation between length of scape ( $x$ ) and length of the bract subtending the lowest flower ( $y$ ) is shown in figure 4. Data for scapes with one flower only have been indicated by open circles, scapes with two or more flowers, by dots. There is a linear logarithmic relationship for the latter group of plots. Applying the formula for heterogonic growth,  $y = bx^k$ ,  $b = 0.023$ , and  $k = 1.2$ , for the Mendon collections. This value of  $k$  means that the lowest bract grows faster, relatively, than the scape.

Data from specimens collected elsewhere in New York State (crosses) show significant deviations from the above relationship, suggesting hereditary differences in the value of  $b$ . A more exhaustive set of measurements from specimens collected over a still wider range would doubtless show still greater deviations. For specimens in the Cornell University Herbarium of the very similar species, *P. Purshii* R. & S., collected from Texas to California north to Michigan and Washington, the relationship between number of flowers and scape length was very distinct for the various geographical localities represented,  $b$  appearing to be the variable rather than  $k$ .

There is an interesting taxonomic consequence of the heterogony of the bracts of *P. aristata*, namely, that depauperate specimens have the lowermost bracts as short as, or shorter than, the flowers which they subtend, the flowers being nearly constant in size. The length of the bracts relative to that of the flowers has been used as a key character to distinguish *P. aristata* from other species within the genus. For example, in the species key in *Grays New Manual* (Fernald & Robinson 1908), plantains with "bracts much exceeding the calyx," and in the *Flora of Indiana* (Deam

1940), plantains with "lower bracts at least twice as long as the flowers" belong to this species rather than to *P. Purshii* or *P. lanceolata*. An examination of figure 5 shows that a fairly high proportion of the smaller plants of the Mendon population possess bracts much less than twice the length of the calyx (all plots falling to the left of the broken line). In this species capsule length is very nearly the same as that of the calyx. Data for collections from other New York localities have been included (crosses).

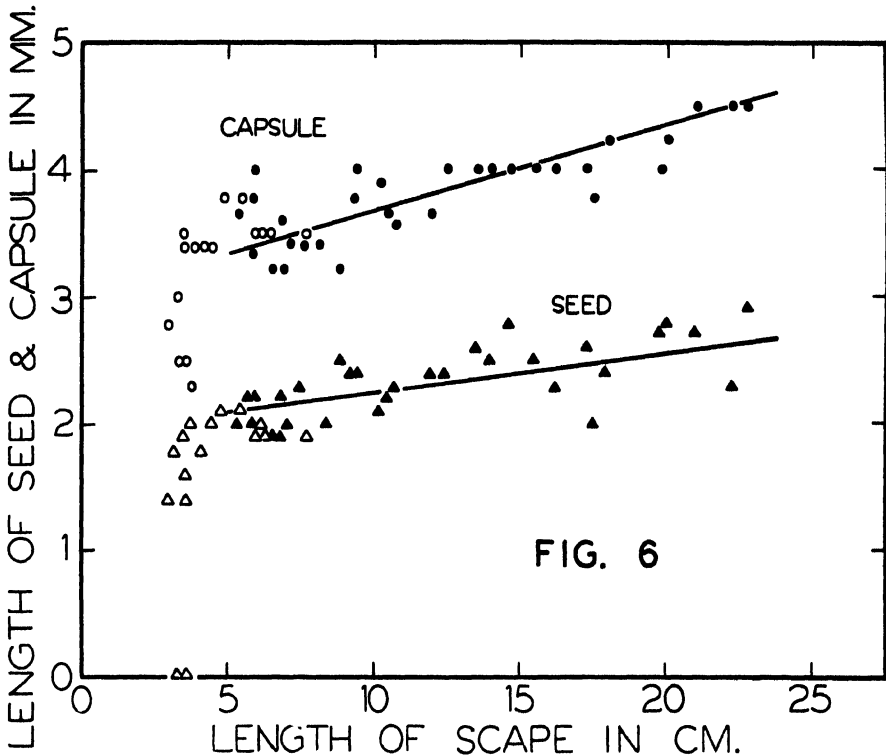


FIG. 6. Length of seed (triangles) and capsule (circles) plotted against length of scape. Open symbols: plants with one flower only; solid symbols: plants with two or more flowers.

Only three of these other collections contained depauperate plants with relatively short bracts. A collection containing only depauperate specimens will probably be a relatively rare occurrence and so may not be too important from the point of view of constructing a key. The taxonomist should bear in mind, however, that variation of this type may be controlled primarily by the size attained by the plant—that it is a dependent and not an independent variable.

The length of seed and capsule have been plotted against length of scape

in figure 6. For plants with more than one flower per scape, there is a definite increase in capsule length (about 30 per cent) and in seed length (about 25 per cent) with increase in length of scape. It should be recalled that length of scape is correlated with the vegetative vigor of the plant. For plants with only one flower per scape there is a rapid falling off of flower and seed size with additional decrease in scape length.

When the plant passes into the reproductive phase of development it evidently utilizes all its available resources in the production of flowers and seeds. The number of flowers produced is dependent upon the extent of these resources; while the size of the individual flowers increases only to a limited extent. Depauperate plants with only one flower, however, can no longer control flower size by varying the number of flowers produced. Everything available goes into the single flower and the two boat-shaped seeds contained within the capsule. If there are insufficient reserves for one full-sized flower, flower size and seed size are reduced; and, in extreme cases, only one of the seeds develops, while the other aborts, or no seeds are produced at all.

From the foregoing analysis, it can be seen that variation in the size of the reproductive structures of *P. aristata* is closely dependent upon the vegetative vigor of the plant. The question may be asked, is this variation in vigor due to heredity or to environment? One bit of evidence has been obtained indicating that variation in vigor, at least, is not primarily genetic. Seeds from plants similar to those shown in figures 1A and 1B were collected, and from them seedlings were grown side by side in the greenhouse. The resulting plants are shown in figures 1C and 1D. It can be seen that both plants are normal and vigorous. Plants from the larger parents were somewhat larger than those from the smaller ones, but this may well be due to the nutritional advantage given to the plants from the larger seeds.

The reason for the great variation in vegetative vigor in the Mendon population of *P. aristata* is not known. One possible explanation might be that in nature there is a difference in the time of germination of the seeds, which, in turn, might be due to a number of different causes, such as depth of the seed in the soil, overturning of the soil in the bridle path by horses' hooves, etc. The seedlings germinating early in the season would have a head start over those germinating later on. If flower induction were photo-periodically controlled in this species, then the size of the plant at the onset of flowering would determine the extent of the reserves available for flower production.

In order to check the above-mentioned hypothesis, seeds were planted in pots and germinated in the greenhouse at monthly intervals from January through April. Germination was somewhat sporadic. All the plants thus

grown flowered in May, regardless of the date of germination. This suggests that *P. aristata* is indeed a long-day plant. The size of the plants varied considerably, but no one-flowered specimens were obtained. The fact that flowering occurred earlier in the greenhouse than it does in nature is doubtless due to some of the many environmental differences between greenhouse and natural conditions.

#### SUMMARY

An analysis has been made of variation in a natural population of *Plantago aristata*. It has been shown that the reproductive capacity of a plant of this species is at least roughly proportional to its vegetative vigor, and that variations in number of flowers, and length of scape, capsule, seeds and bracts are all correlated with this vegetative vigor. The growth of the bracts exhibits a certain amount of heterogony. Differences in size are due chiefly to environmental and not to hereditary factors. The suggestion is made that variation in the time of germination may be responsible for variation in size of the plants at the time of floral initiation, and that a critical long-day photoperiod may initiate flowering in all plants of this species irrespective of their size.

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## EMBRYONIC DIFFERENTIATION IN *TAXUS CUSPIDATA*<sup>1</sup>

CLARENCE STERLING

The development of organized meristems and the differentiation of tissues laid down by these meristems are subjects which have continually interested plant morphologists and physiologists. However, problems of polarity, meristematic structure, and organ differentiation are still far from being satisfactorily resolved. Although various approaches have been attempted, newer techniques are constantly being enlisted in an effort to investigate these questions. In the thought of contributing added data toward a better understanding, the present study considers the histogenetic aspects of meristematic development and tissue differentiation in the late embryo of *Taxus cuspidata*. This investigation is a continuation of the ontogenetic study of early embryogeny in the same species (Sterling 1948b).

**Materials and Methods.** The embryos used in this investigation were obtained from the same source described in the study of gametophyte development (Sterling 1948a), and the killing, fixing, and staining procedures are similar. However, it should be noted here that the Carnoy mixture often caused excessive shrinkage in the cytoplasm. Drawings were made by camera lucida, and photomicrographs were taken with a Leitz "Micam" attachment.

**Initiation of Late Embryogeny.** In the embryo which is becoming massive, growth activity is centered in a small group of initials at the surface of the free apex of that embryo. The initial cells are the progenitors of the other cells in the enlarging, undifferentiated apex. From these initials, all other cells of the embryo appear to diverge in periclinal rows. The anticlinal walls can be envisaged as concentric arcs radiating from the initial region, indicating the successive growth increments in apical development. Thus the free apex of the embryo is organized like the apical meristem of a shoot. At this stage of development, this meristem at the free apex is the only center of mitotic activity in the embryo. Usually, no further cleavage is to be found in the ontogeny of the *Taxus* embryo. However, occasional bilobed embryos have been found at this stage, as has also been reported in *Ginkgo* (Lyon 1904), *Torreya* (Buchholz 1940), and *Welwitschia* (Pearson 1916).

On superficial examination, there can be seen a clear demarcation be-

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tween the parabolic free apex and the columnar suspensor of the embryo. The apical region consists mostly of small cells with deeply-staining, densely-granular cytoplasm and relatively large nuclei. In the suspensor, the cells are immediately distinct by virtue of their large size, their large vacuoles, and their relatively lightly stained cytoplasm. Consequently the majority of the cells of the free apex can be regarded as eumeristem cells. The cells of the initial region begin to stain slightly less intensely than their derivatives, but this difference is not especially marked at first (fig. 13).

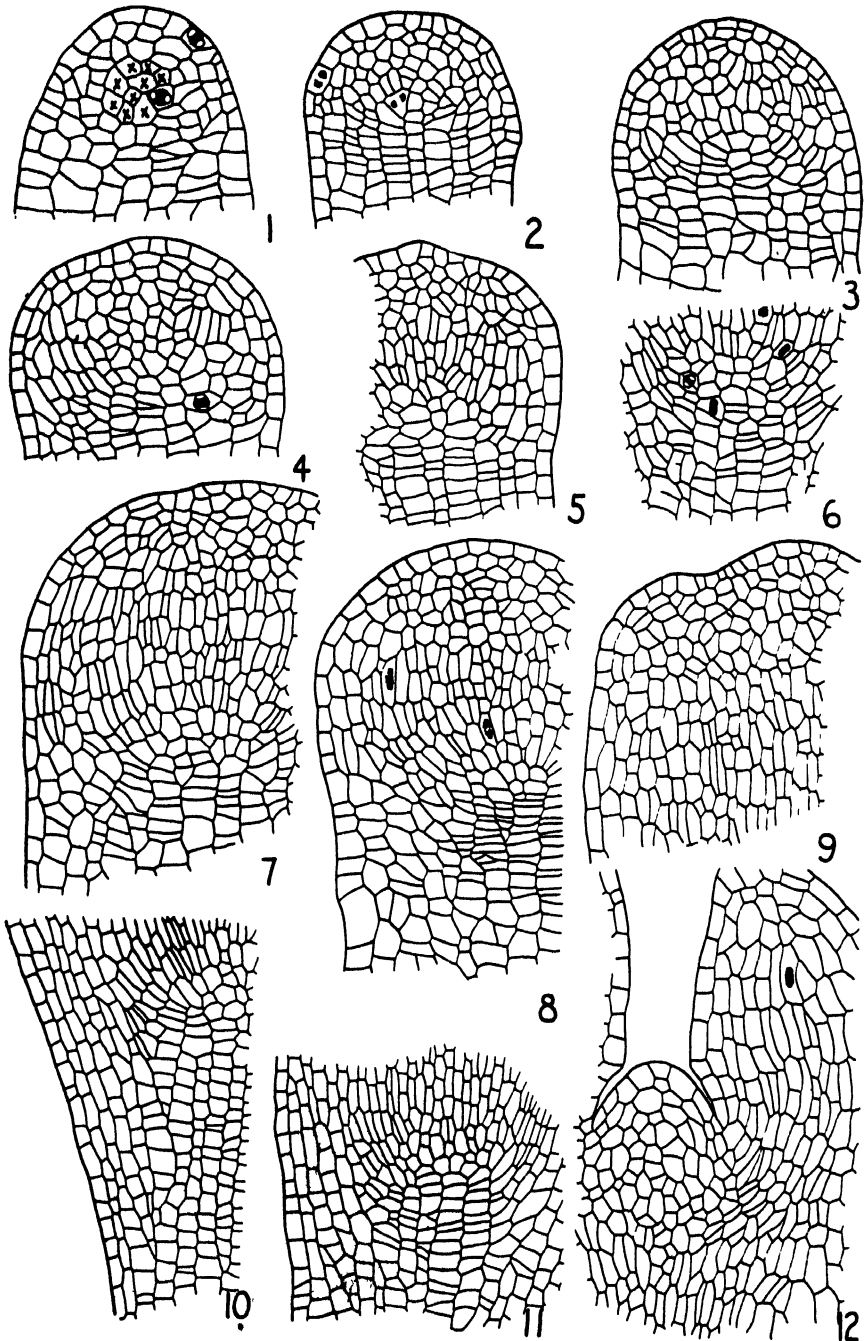
**Meristematic Differentiation.** Within the free apex, a different type of development soon becomes noticeable. In an apparent extension of activity, a deeper center of cell division is produced within the eumeristem tissue a short distance below<sup>2</sup> the summit of the apex (figs. 1, 14, 21). Indicative of such an extension, some apices may show a different quality of cytoplasm in these deeper focal cells, somewhat reminiscent of the central mother-cell zone of the cycad shoot apex (Foster 1941). In this region, the cells stain more lightly than their immediate neighbors. Soon thereafter, the creation of a lower focal zone can easily be ascertained from the change in direction of new cell divisions (figs. 2, 21).

About the more lightly-staining area, particularly at its base and sides, the cells begin to divide with walls which are arranged in the direction of arcs of circles concentric about this region (figs. 2-4). Immediately within the area, the cells at first divide in variously oriented planes, with a seeming tendency for the new walls to lie in arcs about the center (figs. 2, 21). However, as growth proceeds, the cells within the central region divide in planes which are orthogonal to the longitudinal axis of the embryo, like Hanstein's (1868) "Würfelmeristem" or Schüepp's (1926) "massige Meristeme" (figs. 3-5). Towards the periphery of the zone, and immediately outside it, the concentric divisions spread outward to include a continually widening zone of cells.

There has thus been produced a lighter-staining group of central cells which are temporarily active. This group has been designated "stele promeristem" by Allen (1946), and the same term was used by the writer in the study on early embryogeny (Sterling 1948b). However, on the basis of a more critical examination of development in the *Taxus* embryo, the writer now prefers to employ a different expression. In view of the fact that this central area experiences only a limited amount of activity (hence is in the nature of a primary meristem rather than a primordial meristem) and only contributes indirectly to "stele" formation, and because it is located at the

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<sup>2</sup> In the following descriptions, the free apex of the embryo (abmicropylar pole) is considered as its upper end and the admicropylar structures as toward the lower end.



"focus" (Sachs 1878) of various cell series, it might well be called a "focal zone." The organization of this temporarily meristematic region precedes the differentiation of the procambium and the root generative meristem (see below) in the conifer embryo.

At the free summit of the embryo, the superficial cells and the immediately underlying cells divide by anticlines and periclinal, with anticlinal divisions predominating in the surface layer (figs. 3-5). The activity of these cells, which surmount the focal zone, becomes more limited, so that the volume of tissue contributed by their development is only a small percentage of the total at embryo maturity. At the time of organization of the central focal group, these cells above that group contribute to it to some extent. However, as the embryo enlarges, the surface initials become less and less active.

The concentrically dividing cells at the lateral boundaries of the focal zone are arranged early in a cup-shaped group, somewhat flared below the free apex of the embryo (figs. 4, 15, 16). As these cells divide, they become more densely staining than the cells external to them. In this early stage, they are also slightly more tabular. Since these cells possess the histological features of procambial tissue (and later develop the typical functions of that tissue), this bowl-shaped tissue may be referred to as procambium or procambial "cylinder."

Immediately outside the procambial zone, the adjoining cells also experience concentric divisions. In these more lightly staining cells, the new walls are oblique to the original anticlinal walls. Although the cells produced by these divisions enlarge to some extent, divisions occur more rapidly than restitution of cell volume. Thus arcs of narrow cells are produced, which have their greater diameter in the direction of the arc and a smaller diameter in the direction of the focal radius (figs. 3, 4). Inasmuch as the apparent size and shape of the mother cells is maintained initially, it is clear

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#### Explanation of figures 1-12

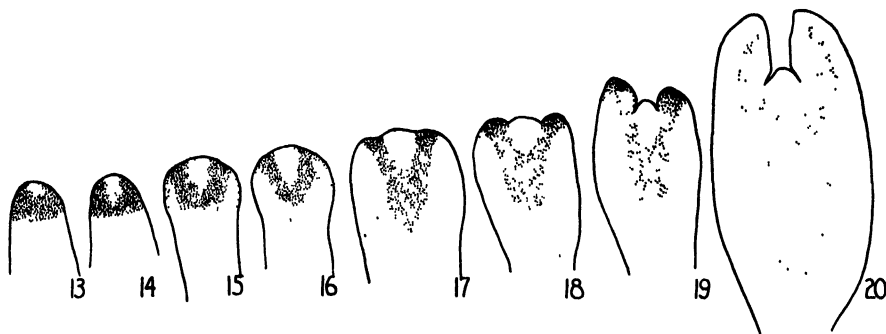
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Camera lucida drawings of longisections of *Taxus* embryos, with micropyle toward bottom of page. All figures  $\times 174$ . FIG. 1. Start of development of focal area below free apex. Focal cells indicated by "x." FIG. 2. Later stage, showing orientation of divisions about focal group. FIG. 3. Enlargement of cells in focal area, with indication of "Würfelmeristem" divisions here. Concentric divisions about focal group becoming marked. FIG. 4. Root generative meristem becoming active. Concentric divisions on lateral borders of core area are increasing the number of cortical layers. FIG. 5. Early start of formation of conical shoot apex in this embryo. Procambium becoming more distinct at sides of focal group. FIG. 6. Active root generative meristem in stage of about that of fig. 19. FIG. 7. Formation of buttress of presumptive cotyledon. FIG. 8. Procambial core becoming active behind root apical meristem. FIG. 9. Initiation of cotyledonary primordia. Note subepidermal activity. Shoot apex enlarging. FIG. 10. Region in vicinity of root generative meristem of large, near-dormant embryo. Absence of column and pericolumn is characteristic. FIG. 11. Region of root generative meristem of embryo in stage of fig. 29. FIG. 12. Shoot apex of mature embryo.

that the form of the daughter cells is not the direct result of a growth pressure by the central area.

Because cell divisions in the focal group occur in three orthogonal planes and since the newly formed cells here tend to enlarge to the size of the parent cells, the focal area enlarges, and its growth produces a swelling in the diameter of the embryo at the free apex (figs. 4, 5, 15, 16). The earlier-mentioned concentric divisions outside the focal region do not extend to the superficial layer of the embryo. Hence, as the internal tissue increases in volume, the outermost stratum accommodates to the increasing surface area by anticlinal divisions primarily. Few or no periclinal divisions occur in this superficial layer, so that its individuality is preserved (figs. 3-5, 7, 8, 26).

Below the focal area, tabular cells arranged in arcs are also to be found,



Outline drawings of *Taxus* embryos in longisection. Density of stippling indicates relative staining intensity. Micropyle toward base of page. All figures  $\times 45$ . FIG. 13. Embryo before differentiation of central focal group. FIG. 14. Focal group differentiated. FIG. 15. Enlargement of embryo apex. FIG. 16. Start of formation of massive embryo. FIG. 17. Initiation of cotyledonary primordia. FIG. 18. Enlargement of cotyledon primordia. FIG. 19. Stage somewhat prior to that of fig. 24. FIG. 20. Mature embryo. Cf. figure 12.

but in this region, the direction of the concentric walls coincides with that of the original transverse walls in these cells. Here divisions of the rib-meristem type are numerous, and the cells have a very small longitudinal diameter in comparison with their transverse diameter (figs. 3-6, 21).

Just above this rib-meristem region, in the base of the focal area, is found a group of cells which remain slightly larger than their neighbors and slightly lighter-staining (figs. 5, 6, 8). Their large nuclei become prominent and noticeably spherical, but their chromatic material does not stain quite as intensely as that of the nuclei of adjoining cells. The group is further distinguished by the fact that its cells soon play the role of initial mother cells in the further development of the lower part of the embryo. Consequently, this region has been characterized by Schopf (1943) as gene-

rative meristem and by Allen (1946) as root generative meristem. When developmental series are studied, it can be seen that this initial zone is differentiated in contact with the cylinder of procambium which has been formed on the sides of the focal region.

**Production of the Massive Cylindrical Embryo.** After the differentiation of the procambial cylinder and the root generative meristem, the suprasuspensor region of the embryo enlarges notably (figs. 7-9, 17, 18, 22, 26). The predominant increase in size occurs in the direction of the longitudinal axis. Just above the root generative initials, transverse divisions occur less rapidly than cell elongation, and longitudinal divisions in various planes become quite frequent. Hence, these cells become narrower and more elongate, remaining densely-staining as the surrounding cells begin to stain less intensely. In this manner, the cells of the lower part of the focal zone, just above the root generative meristem, acquire a definite procambial aspect.

These cells are the first procambial cells of the central core common to hypocotyl and root. They are formed in continuity with the procambial cylinder about the original focal group, being produced as the cells in the upper part of the focal zone become inactive. Between the two procambial zones, the region of juncture is V-shaped in longisection. Once formed, the procambial core experiences numerous longitudinal divisions, relatively fewer transverse divisions, and continuous cell elongation. Because of the future more or less autonomous growth of this central procambial strand, it might seem to deserve the name "stele promeristem" of Allen (1946). However, as a result of a critical examination of the stelar concept (Sterling 1949), it would seem more proper to designate the tissue in question as a procambial core, or simply procambium, as was done by Miller and Wetmore (1945).

At a slightly more advanced stage, the lower cells of the procambial core can be seen to converge definitely toward the initials of the root generative meristem. The arrangement of these cell lineages and of the division figures indicates the derivation of the lower procambial area from the root generative meristem (figs. 6, 26). That meristem can also be seen to give rise to many of the longitudinal files of cells in the young cortex immediately adjoining the procambium. In addition, the central rows and some more peripheral rows of suspensor cells obviously owe their origin to activity in the initials of this meristem.

The outermost layer of cells in the embryo exists as a discrete stratum (protoderm) below the flanks of the free apex, and it can be followed as such far down into the suspensor. Likewise, two or three hypodermal layers also appear to form a continuous, uninterrupted mantle (figs. 22, 26). These layers are perpetuated by anticlinal divisions mainly and are not re-



newed by the activity of the root generative meristem. However, occasional periclinal divisions may be seen in any of the young cortical layers, and the concentric divisions continue outside the upper part of the procambium to form additional cortical layers and thus increase the embryo diameter (figs. 7, 8).

As the procambial core region enlarges and elongates, a few more rows of cells are formed outside it in the cortex by the root meristem. The cells cut off along the lower edges of this meristem are shifted to the side by the continued advance of the meristem as well as by further lateral divisions in the meristematic cells. Consequently the new, centrally placed initials take over the meristematic function, and the more laterally situated ones (together with their derivative rows of cells) are displaced from the axial line to contribute to the embryonic cortex (figs. 6-8). Transverse divisions begin to occur more regularly in the displaced lineages as rib-meristem activity is initiated in the cortex.

**Cotyledon Formation.** As described above, the cells in the superficial layers of the embryo divide primarily by anticlinal below the summit of the free apex. At the very summit, periclinal divisions are also frequent. Just below the apex, longitudinal divisions in the procambial cylinder and tangential divisions in the surrounding cortex, together with subsequent cell enlargement, produce an increase in embryo breadth. Thus broad shoulders are formed on the flanks of the free apex, and it is from these shoulders [equivalent to Louis' (1935) foliar buttresses] that the cotyledonary primordia are formed (figs. 7, 9, 17, 18, 22, 26). The two (or three) cotyledon emergences arise by active periclinal divisions in the hypodermal layer of cells at the buttresses. Although the surface layer may also undergo periclinal divisions, these seem far less significant than those in the subjacent layers in contributing to the volume of the emergence.

With regard to the procambial strands which supply these cotyledon primordia, it is interesting to note that there is here no question of acropetal or basipetal differentiation. As was pointed out above, the procambial cylinder is produced as a deeply-staining, cup-shaped zone following its initial differentiation. The upper edges of this cup rest against the flanks

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#### Explanation of figures 21-26

Photomicrographs of longisections of *Taxus* embryos, with micropyle toward base of page. FIG. 21. Embryo just after differentiation of focal area. A few concentric divisions have occurred.  $\times 312$ . FIG. 22. Initiation of cotyledonary primordia. Note continuity of deeply-staining cells from central procambium into cotyledon.  $\times 152$ . FIG. 23. Root generative meristem of near mature embryo.  $\times 312$ . FIG. 24. Near mature embryo.  $\times 71$ . FIG. 25. Shoot apex of mature embryo.  $\times 125$ . FIG. 26. Off median section of embryo which is forming cotyledonary buttresses. Flared upper edge of procambial region not shown in this view of edge of central procambium.  $\times 152$ .



of the free apex of the embryo, and it is in conjunction with these regions of the procambial core that the cotyledonary primordia are initiated. Hence, the procambium of the embryonic body is blocked out as a unit before the formation of cotyledons and presages the future appearance of the latter (figs. 14-18).

At their first appearance, the procambial traces at the cotyledonary node are distinct only by virtue of their deeply staining cells and their more or less oblique course (figs. 19, 29). The enlargement of the cotyledonary primordia is attended by the elongation of the cells of their incipient bundles, so that the aspect of the latter becomes more and more definitely procambial, resembling closely the cells of the procambial core of the hypocotyledonary body (fig. 24). Outside the bundle, the cells of the cotyledons stain far less intensely and are more isodiametric than those of the procambium. Apical growth of the cotyledons continues in a small group of superficial initials which give rise to anticlinal and periclinal derivatives. The other surface cells of the cotyledons divide anticlinally alone, thus continuing the hypocotyledonary protoderm over most of the surface of the embryo.

**Embryo Maturation.** Once the various meristems have been organized and cotyledonary primordia produced, further development in the yew embryo involves principally an enlargement and a slight amount of further tissue differentiation in the different regions of the embryo. Although the cotyledons elongate somewhat, their length growth subsequent to their formation is not so great as that which takes place in the hypocotyl. Behind each growing cotyledon apex, a single procambial strand differentiates acropetally.

The embryo apex, which is a remnant of the original broader summit, may be considered as a minimal surface following cotyledon formation (figs. 12, 25). It is now definitely the shoot apex of the embryo. In this apex, the constituent cells stain far less intensely than the other cells nearby and are much larger and more isodiametric. Very little mitotic activity is displayed in this shoot apex of the maturing embryo. However, as the cotyledons enlarge and elongate, the shoot apex slowly enlarges to form a conical mound of tissue between them. Although no mitotic figures could be found in this growth, the increase in the number of cells indicates that some cell divisions have taken place.

Development in the hypocotylary region involves a great amount of cell division and elongation to produce the rather long body of the embryo. The procambial tissue in the center (figs. 23, 24, 28, 32) is composed of very narrow, elongated cells in rows which are traceable down to the root generative meristem. Divisions in the procambial core continue in the pattern followed before cotyledon initiation, viz., some transverse divisions and

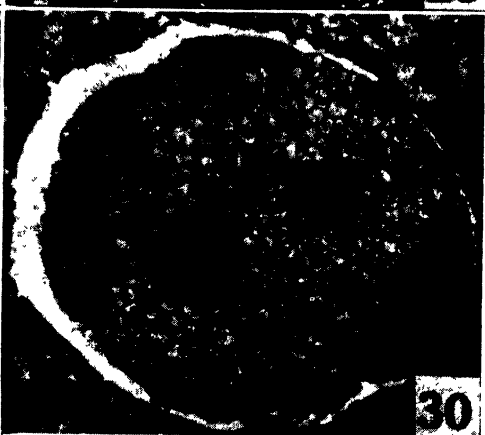
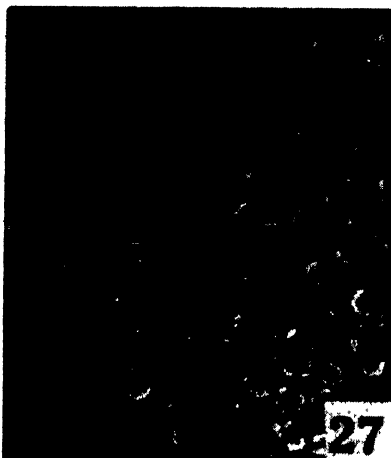
many longitudinal divisions in various planes. Thus, a cell which is cut off by the meristem toward the procambial area by a transverse division elongates in the long axis of the embryo and undergoes longitudinal divisions. Later, transverse walls may also be formed. Throughout the core area, these orthogonal divisions may take place at any distance from the root generative initials, so that the procambial core increases in volume autonomously.

However, those cells produced by the peripheral initials of the root meristem divide in a different fashion. In these cells, the subsequent divisions are more or less tangential. As the cell lineages are traced upward from the meristem, more and more tangential walls may be seen to be formed, increasing the number of cells at each successive level above the meristem—up to about four or five cells arranged in radial rows. The cells in these rows are intermediate in staining intensity between the cortical and the procambial cells. After germination, they may develop into so-called pericyclic tissue [said by Strasburger (1872) to consist of 2–5 rows of cells in the primary body of the root]. However, there are no precise divisions in the initials, nor does the subsequent ontogeny set off this region from the others produced by the root generative meristem. Even in a mature or almost mature embryo, these rows are definitely transitional between procambium and cortex in histology and mode of origin (fig. 23).

Since transverse divisions are relatively more numerous in the cortical area, the cells do not reach the length of the procambial initials. Occasional longitudinal divisions are to be noted in this stage of cortical development, but these are relatively rare in comparison with those transverse to the long axis of the embryo. Superficially, the rows of cortical cells appear to extend in lines continuous over the tip of the root generative meristem, but in actuality this configuration is due to the production of derivatives in radiating rows by the various initials of the root apical meristem and the gradual lateral displacement of these rows as the meristem advances and produces more of these rows of derivatives. Thus is created the “coaxial” pattern characteristic of a root apex.

Apparently the root generative meristem itself does not stand out very clearly. Its cells are arranged in a sort of horizontal disk, which is transverse to the longitudinal axis of the embryo (figs. 23, 27, 32). The initials are slightly larger than their derivatives, somewhat lighter-staining, and so situated that their derivatives can be seen to radiate out in all directions. Although divisions are not so frequent in the root generative meristem as in the cells cut off by it, they have been noted in fair abundance.

The root generative meristem furnishes cellular components not only for the body of the root but eventually also for most of the root cap-suspensor tissue. The suspensor is first produced by uniform rib-meristem activity behind the free apex of the young embryo (Sterling 1948b). Even after



the initial organization of the root generative meristem, the production of suspensor tissue (unlike that in the Pinaceae) follows this same pattern of uniform longitudinal rows of cells arranged parallel to the long axis of the embryo.

During the growth of the central procambial core, the activity of the root generative meristem in the admicropylar direction is not particularly marked. Consequently, as the procambial core enlarges, a difference in diameter becomes apparent between the hypocotyl and the suspensor. After the initiation of the cotyledon primordia, the activity of the root apical initials in the direction of the suspensor begins to increase slightly (figs. 10, 11, 32). In this manner, longitudinal rows of cells are produced directly below the meristem, seemingly set off more or less distinctly from those rows continuous between cortex and suspensor. However, the rows of root cap cells are rather short in comparison with the length of rows in that region in other conifer embryos, and they are not distinguishable from the suspensor proper.

**The Mature Embryo.** At maturity, the embryo does not differ markedly from its earlier appearance as described in the discussion of the maturing embryo. Suffice it to remark that the shoot apex is rather large, consisting of more or less isodiametric, lightly staining cells which appear to be inactive. Below this apex, a lightly staining region extends down a short distance into the procambium of the hypocotyl, perhaps as the equivalent of the more extensive medullary region of the pinaceous embryo (figs. 12, 20, 25). There is no definite pith, nor are secretory elements differentiated.

The two or three cotyledons (fig. 31) are relatively short, and their procambial strands (fig. 30) are strongly arched as they depart from the hypocotylary procambium (fig. 25). Neither in cotyledon nor in hypocotyl is there any vascular differentiation in the mature embryo. An epidermis is continuous over the mature cotyledons from the shoot apex to the hypocotyl, extending down over the hypocotyl as a uniseriate layer into the root capsuspensor region (fig. 32). Several hypodermal layers also appear to exist as continuous strata between hypocotyl and suspensor.

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#### Explanation of figures 27-32

Photomicrographs of *Taxus* embryos. In longisections, micropyle is toward bottom of page. FIG. 27. Cross section through root generative meristem of near mature embryo.  $\times 208$ . FIG. 28. Cross section of hypocotyl of mature embryo about level of top of figure 32, showing central procambium.  $\times 125$ . FIG. 29. Longisection showing enlargement of cotyledon primordia. Note how gametophyte tissue has been digested in advance of embryo.  $\times 125$ . FIG. 30. Cross section near insertion region of the two cotyledons. The procambial strands are indicated by arrows.  $\times 125$ . FIG. 31. Cross section through shoot apex of tricotyledonous embryo.  $\times 125$ . FIG. 32. Lower part of near mature embryo, showing presence of several superficial cell strata continuous from hypocotyl to suspensor.  $\times 125$ .

As in the prothallium, most of the cells of the embryo (with the exception of the procambium and the initial regions of root and shoot) are filled with ergastic contents, which are probably food reserves of some sort. It may be noted that while the initials of the root generative meristem are lightly-staining, they are neither as large nor as conspicuous as the shoot initials. The root apical initials are distinguishable from their derivatives only with difficulty in the mature embryo.

Surrounding the embryo is the large, pear-shaped mass of gametophyte tissue which has been enlarging simultaneously with the embryo. Development of this tissue appears to follow Jäger's (1899) description, with the multiplication of nuclei within its cells and further aberrant behavior, including fusion of these supernumerary nuclei. The cells of the gametophyte are large, multinucleate, and filled with spherical bodies of various ergastic materials. No microchemical tests were performed on the prothallial tissue to determine the nature of these cell inclusions.

**Discussion.** Attempts to explain the organization of a meristem in terms of the cell lineages which are a product of that organization can reach only a certain level of understanding. Such a level was virtually attained in the geometrical constructions of Sachs (1878, 1879). Although further refinements were introduced by Reinke (1880) and Schüepf (1926, 1946), their emendations have contributed more to a better analysis of the mechanics of growth than to an understanding of the causal factors in the organization of a plant meristem. However, it should be noted that, although describing meristematic activity in terms of cell lineages, both Sachs (1878, 1879) and Hanstein (1868) particularly stressed the fact that cell lineages were only a function of growth and organization in the meristem and not their determinant, that rather the inherent potentialities of the plant determined the patterns of cell division and cell elongation.

In his analysis of meristem structure, Sachs (1878) made a signal contribution which has been conspicuously neglected in later investigations. Sachs described the point about which anticlinal and periclinal cell rows were arranged as the common geometrical *focus* of these parabolic curves. Interestingly enough, this focal point was not always to be found among the initials themselves but sometimes lay deeper in the meristem, along its axis of growth. Coincidentally, in discussing the apical cell in cryptogams, Sachs showed that the focus lies in the apical cell itself and that this cell is the slowest-growing portion of the meristematic apex.

In addition to Sachs' observation, this phenomenon of diminished activity in a focal region may be seen to obtain in the apex of the root of *Angiopteris* (Schwendener 1882; Koch 1895). Similarly, the large-celled central mother cell group in the shoot apices of *Ginkgo* (Foster 1938) and the

cycads (Foster 1941) may be shown to be in the focal area. The same phenomenon appears in various conifer shoot apices (Sterling 1945, 1946) and root apices (Janczewski 1874; Flahault 1878; Schopf 1943), and recently Philipson (1947) has reported essentially this structure in the angiosperm shoot apex.

If it be accepted that the large size of the cells in a focal area reflects a diminution of meristematic activity (and perhaps growth also), a common quality seems to inhere in the apices of at least the gymnosperms and the lower tracheophytes. The apical meristems of root and shoot in these plants are alike in that the focus of growth (as defined by Sachs) is a region of minimal activity. The cell or cells in the focal area are generally larger than their neighbors, experience relatively fewer mitoses, and possess larger vacuoles in their cytoplasm. Their protoplasmic regions stain less intensely than those of surrounding cells, and their walls may be thicker. This anomaly of a functionally less active area as the central core of a developing meristem may be explicable in terms of diffusion gradients, oxygen supply, growth hormone production, hydrion concentration, etc. and perhaps also with respect to physical forces.

Immediately around the focal area the meristematic cells are smaller, thinner-walled, actively dividing, and have a higher nuclear-cytoplasmic ratio. This eumeristem tissue divides orthogonally with respect to the boundary of the focal zone, i.e., divisions in these cells are tangential and radial to the periphery of that zone. This tissue constitutes the segmentation zone of the lower tracheophytes and may be noted outside the focal zone in gymnosperm apices. Thus it is possible to visualize the focal region as a center of growth activity, from which cell lineages diverge in all directions and experience a more rapid mitotic activity than obtains in the cells of the focal region.

The organization of meristematic activity in the *Taxus* embryo appears to be based on the distribution of "focal zones." In this embryo, the differentiation of a central focal area below the free apex is related to the initiation of meristematic (and tissue) differentiation in further development. The cells above this zone (toward the free summit) continue as initials of the embryo shoot pole. The cells dividing laterally to this region constitute the precursor of the upper procambium and cortex; and the cells at the base of the focal zone initiate the body of the root and the root capsuspensor tissue. As the cells in the upper part of the focal group become dormant, activity is continued in the lower cells of the zone, these cells becoming the initials of the root generative meristem. Such a relationship seems to occur also in the embryos of cycads (Guttenberg 1941) and *Ginkgo* (Lyon 1904; Sprecher 1907).

In connection with the zonal structure of the meristems in the embryo might be mentioned the phenomenon of procambial differentiation. Although the procambium in *Taxus* develops as a more or less central core of tissue which is continuous throughout the embryo axis at its initial differentiation (also *Phlox* of Miller & Wetmore 1945), Schopf (1943) describes it as appearing first at the node ("nodal meristem") in *Larix* and differentiating up into the cotyledons and down into the hypocotyl from that region. Likewise, Buchholz (1919) notes a late development of vascular strands after the start of cotyledon elongation in the pine embryo.

Despite the extensive comparative treatment of conifer embryogeny by Strasburger (1872) and Kapfer (1935), one or two features of the late embryogeny of *Taxus* justify a comparison with embryo development in other conifers. The most striking characteristic of the yew embryo is the relatively minor development of its root cap-suspensor region. This phenomenon was described in the embryo by Reinke (1873) and in the adult root by Strasburger (1872), Reinke (1873), and Janczewski (1874); it occurs also in the roots of *Cycas circinalis* (Reinke 1873), *Ginkgo* (Strasburger 1872), *Sequoiadendron* (Schwendener 1882), and *Biota* (Flahault 1878). In the *Taxus* embryo, the interesting feature of this limited development of the root cap is that, as a consequence, there are (1) series of continuous superficial cell strata extending from cotyledon into suspensor and (2) no "juncture zone" between the body of the root and the root cap, such as characterizes the pinaceous and cupressad embryos (Strasburger 1872; Buchholz & Old 1933; Kapfer 1935; Cook 1939; Schopf 1943; Allen 1947; Wang 1947).

Soon after the differentiation of the root generative meristem in the Pinaceae, there occurs a remarkable, virtually *autonomous* development (as described by Reinke 1872 and Kapfer 1935) in the root cap-suspensor region to form a "column" and "pericolumn" (Schopf 1943). Only after this development has been initiated, does the hypocotylary region begin to elongate. In fact, in *Keteleeria* (Wang 1947) there appears to be little or no subsequent enlargement of the hypocotyl despite the extensive growth of the root cap-suspensor. On the other hand, in *Taxus* the development of the hypocotyl is continuous upon the differentiation of the root generative meristem. Only later is the root cap region formed by this meristem, and this cap constitutes a minor portion of the embryo, consisting of but a few longitudinal cell rows. Kapfer (1935) describes the very narrow root cap-suspensor but fails to mention the continuous protoderm.<sup>3</sup>

On the whole, the pinaceous embryo is characterized by the presence of

<sup>3</sup> Apparently a "rhizodermis" (Allen 1947) develops with regular root activity, which involves the sloughing off of the root cap and the outer layers of the cortex (Strasburger 1872).

a pith and secretory elements (Hutchinson 1917; Buchholz & Old 1933; Kapfer 1935; Schopf 1943; Allen 1947; Wang 1947). Although Kapfer has reported resin canals in *Taxus baccata*, neither these nor a pith could be detected in the embryo of *T. cuspidata*. The yew embryo agrees with all conifer embryos heretofore studied in the presence of a relatively large, rather inactive shoot apex, in the manner of origin of the different tissue regions of the embryo, and in the nature of growth of the root generative meristem. Generic differences may occur in the number of vascular strands which supply the cotyledons, but within certain limits, the total number of strands and of cotyledons formed appears to be a matter of nutritional relationships, whose effect is also expressed in embryo size (Hill & de Fraine 1913; Buchholz 1946).

#### SUMMARY

Meristematic development and tissue differentiation is described in the embryogeny of *Taxus cuspidata*. After apical growth has occurred for some time in the young embryo, the differentiation of a focal area of lighter-staining cells just behind the apex foretokens the formation of the root generative meristem and procambium. The focal area enlarges, and adjacent cells divide with walls concentric about this area. Simultaneously, the root generative meristem becomes active, furnishing abmicropylar cells which contribute to the formation of hypocotylary procambium and admicropylar cells which contribute to cortex and suspensor.

As the focal group becomes less active, the cells produced by the lateral concentric divisions build up buttresses of tissue on the flanks of the free apex of the embryo. Deeply-staining cells in these buttresses have a histological continuity with the cells of the elongating procambial core of the hypocotyl. Although later cotyledon growth occurs by activity of superficial initials, cotyledonary primordia are raised from the buttresses by predominantly subepidermal activity. The procambial strand in each cotyledon, always continuous with the procambial core, develops acropetally behind the apex of the cotyledon.

Only after marked hypocotyl elongation and cotyledon enlargement does the root generative meristem produce any tissue resembling the "column" of the pinaceous root cap. This tissue is very indistinct, and as a consequence of this type of development, there is no "junction zone" on the outer surface of the embryo, and the epidermal layer and several hypodermal layers are continuous from the cotyledons into the suspensor.

As in other conifer embryos, the shoot apex is a conical mass of apparently dormant cells, which are large and have a lightly-staining cytoplasmic matrix. The ripe embryo lacks vascular and secretory elements, and



no pith is present. The cotyledons, usually two in number (sometimes three), are relatively short.

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## CASPIARIAN STRIPS IN ISOETES MACROSPORA

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In longitudinal and cross section through the stem and leaf base region of *Isoetes macrospora* Dur., stained with crystal violet-iodine, the cells of the ligule are found to contain stored material which is greater in amount than in other parts of the plant.

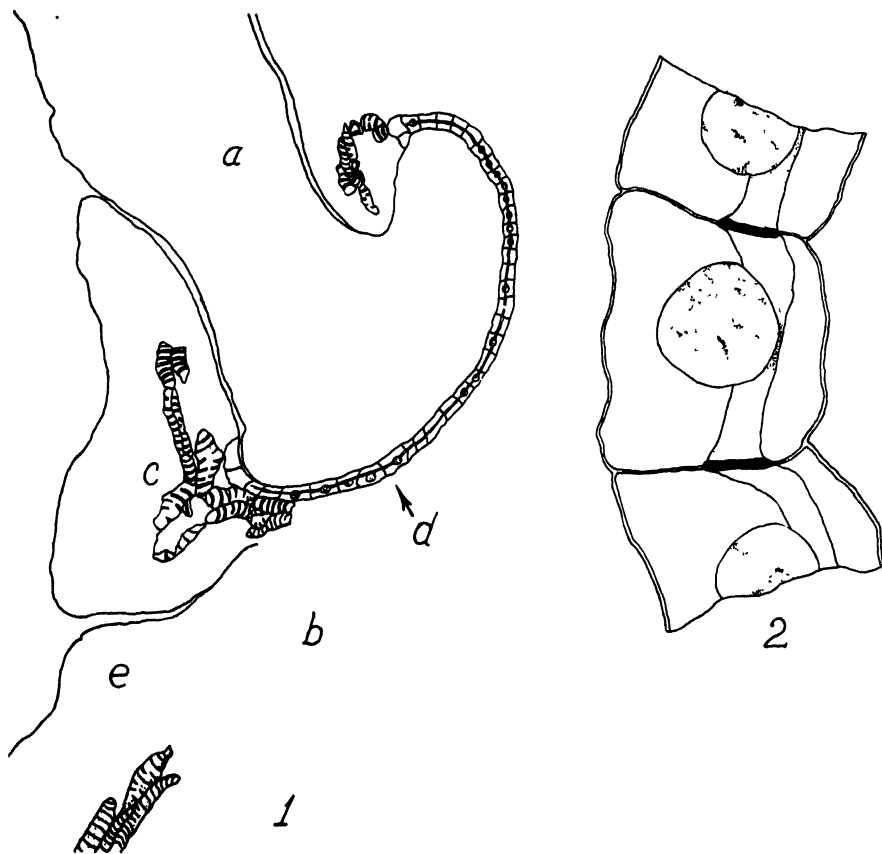


FIG. 1. *Isoetes macrospora* Dur. a, ligule. b, leaf base. c, velum and vascular tissue. d, endodermal-like layer. e, region of sporangium initials. FIG. 2. Enlarged view of endodermal-like cells showing caspian strips.

A superficial layer of cells of the leaf (fig. 1, d) is conspicuous lining the cavity in which lies the imbedded part of the ligule (fig. 1, a). The cells

of this layer are smaller than the adjacent leaf cells and in general are rectangular in sectional view. The radial walls of each cell of the layer possess casparian strips (fig. 1, d), and in section the layer closely resembles the endodermis of some angiosperm roots.

The function of these endodermal-like cells with their casparian strips is not clear, although the difference in amount of deposit and the location of the tissue would suggest that the endodermal-like layer may be involved in the concentration of materials in the ligule.

Similar unequal deposition of material was observed in *Selaginella rupestris* (L.) Spring. where at fairly early stages of development the ligule appears relatively free of stored material, but as development proceeds most of the cells stain heavily, whereas in tissue of leaf, stem, and sporangium adjacent to the ligule the stain is light so that contrast between the ligule and adjacent tissue is marked.

Here as in *Isoetes macrospora* there is a modification found in the leaf cells that ensheath the ligule base. Early in their development the protoplasts of the elongate sheath cells deposit a casparian-like, but less conspicuous, strip on their radial walls.

#### CONCLUSIONS

1. True casparian strips are present in cells of a specialized layer of the leaf at the ligule base of *Isoetes macrospora*.
2. Groups of tracheids are found in contact with the endodermal-like layer that ensheaths the ligule base.
3. Histologically the endodermal-like layer of *Isoetes* and the endodermis of some angiosperm roots might reasonably be compared.
4. Evidence of physiological similarity is insufficient.

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## AN ADDITIONAL REPORT ON THE GROWTH OF EXCISED TOMATO ROOTS

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The excised tomato roots isolated September 29, 1935, and maintained in culture since that time are now in their 144th passage. For the last 131 passages one set of roots has been maintained in a solution limited to mineral salts, cane sugar, and thiamine. Another set was maintained in a solution of mineral salts, cane sugar, and thiazole.

The present paper reports results on the relation of temperature and age of inoculum to the beneficial effect of pyridoxine and the present status of the roots which have been continuously cultivated in solutions supplemented with thiazole.

**Temperature and the Effect of Pyridoxine.** We have demonstrated earlier that pyridoxine improves the growth of this strain of tomato roots provided there is present in the medium an adequate supply of thiamine. Our strain of tomato roots is unable to synthesize thiamine. When thiamine is supplied, growth is limited because of the inadequate amount of pyridoxine synthesized by the root from the basal constituents of the medium. The addition of pyridoxine to the medium containing thiamine results in a substantial increase in growth. We do not know what limits growth in solutions containing both thiamine and pyridoxine. This strain of roots does not respond to nicotinic acid.

Our present concern was to determine whether differences in incubation temperature materially affected the response to pyridoxine.

In a preliminary experiment, roots incubated at 30° C did not survive. We therefore chose 15°, 20°, and 25° C as the temperatures of incubation. Roots were grown individually in 150 ml. Erlenmeyer flasks in 50 ml. of modified Pfeffer's solution containing 1 per cent cane sugar and supplemented with 10 m $\mu$  moles of thiamine and 50 m $\mu$  moles of pyridoxine. Details of the preparation of the solutions have been given earlier.

Each treatment was replicated 15 times and carried out in two series. For one series, the inoculum was obtained from passage 122 in thiamine solution when that passage was 28 days old. The roots in this series were allowed to grow at the three temperatures for 57 days, removed, washed with distilled water, dried at 100° C for 24 hours and weighed. For another series, the inoculum was obtained from passage 123 in the thiamine solution when the passage was 41 days old. Dry weights of the roots in this series were determined after 30 days growth.

Growth in the solutions containing thiamine and pyridoxine was 2-4 times that in the thiamine solutions at 15°, at 20°, and at 25° C (fig. 1). Although growth at 15° C was quite slow, the beneficial effects of the pyridoxine were quite definite.<sup>1</sup> A temperature of 25° C was somewhat better than 20° C for growth in the solutions supplemented with thiamine and in those supplemented with thiamine and pyridoxine. The heaviest

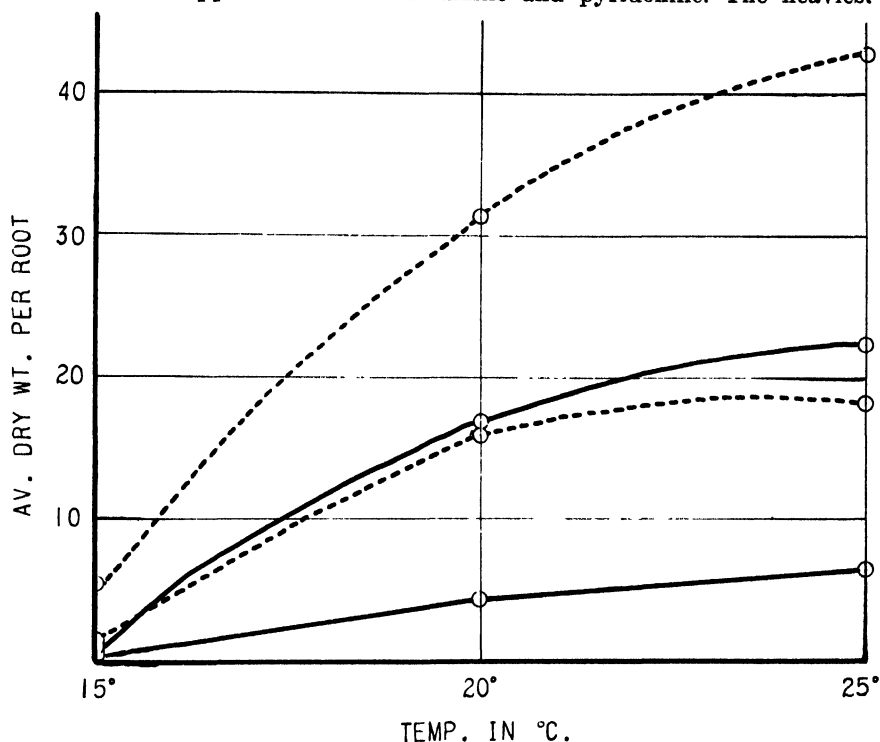


FIG. 1. Average dry weights of tomato roots grown in mineral salts and 1 per cent cane sugar at 15°, 20° and 25° C; solid line below, for 30 days in solutions supplemented with thiamine; solid line above, for 57 days in solutions supplemented with thiamine; dotted line below, for 30 days in solutions supplemented with thiamine and pyridoxine; dotted line above, for 57 days in solutions supplemented with thiamine and pyridoxine.

root weighed 55.8 mg. and was grown in 57 days at 25° C in the solution supplemented with thiamine and pyridoxine. The heaviest root in the solutions supplemented with thiamine weighed 24.1 mg. The weights were greater at the end of 57 days than at the end of 30 days.<sup>2</sup>

<sup>1</sup> For roots grown 57 days, the average dry weight at 15° C in the thiamine solutions was 1.4 mg.; in the solutions supplemented with thiamine and pyridoxine, it was 5.6 mg.

<sup>2</sup> Roots allowed to grow for several months at 20° C in the dark in 50 ml. of Pfeffer's solution with 1 per cent cane sugar and 10 mμ moles of thiamine have reached average weights of 60 to 80 mg. For example, 28 roots averaged 80.9 mg. after 7 months.

In the experiment described, inoculum 28 days old was used in one series and in the other the inoculum was 41 days old. Does the age of the inoculum affect the final dry weights?

**Age of Inoculum.** To determine whether the age of the inoculum appreciably affected the final dry weights obtained in solutions supplemented with thiamine or with thiamine and pyridoxine, an effort was made to obtain inoculum as uniform as possible except for differences in age in the passage from which inoculum was obtained.

Some 44-day-old inoculum was prepared by transferring root fragments on September 21, 1946, to the nutrient solution supplemented with thiamine and incubating at 20° C in the dark. These fragments were obtained from passage 126 when it was 39 days old. After 44 days, fragments

TABLE 1. *Growth of excised tomato roots of various ages in solutions supplemented with thiamine or thiamine and pyridoxine.*

Supplement	Temp. ° C.	Age of Inoculum Days	No. of Roots Weighed	Av. dry wt. mgm.	Range mg.
Thiamine	20	14	15	15.1	9.0-20.2
	20	32	15	18.8	11.8-27.7
	20	44	15	24.5	18.7-39.7
	25	14	15	11.1	7.1-19.1
	25	32	15	21.1	11.3-28.6
	25	44	14	20.7	13.0-28.3
Thiamine and Pyridoxine	20	14	14	30.7	21.3-44.8
	20	32	14	35.6	22.3-50.1
	20	44	15	36.0	27.9-47.6
	25	14	15	37.7	31.5-65.1
	25	32	14	44.5	32.2-54.0
	25	44	15	38.5	19.5-75.2

of the roots in the passage inoculated September 21st were transferred to the nutrient solution containing thiamine and to the solution supplemented with thiamine and pyridoxine. Some of the flasks were incubated in the dark at 20° and some at 25° C.

The 32-day-old inoculum was obtained by transferring on October 23, 1946, fragments of some of the roots of September 21st to solutions supplemented with thiamine or with thiamine and pyridoxine and incubating at 20° and at 25° C.

The 14-day-old inoculum was obtained by first inoculating thiamine solutions on October 21st with root fragments from the cultures of September 21, 1946. The cultures of October 21st were then used on November 4th as inoculum for the thiamine series.

In the procedures outlined above, the passages from which the 14-, 32-, and 44-day-old inoculum was obtained were all inoculated with fragments

of excised roots which had grown for approximately 1 month in a thiamine solution at 20° C in the dark.

Each treatment was replicated 15 times, and the roots were grown at 20° and 25° C in the dark for 2 months.

Growth (dry weights) obtained from the 14-day-old inoculum was consistently less than that from the 32- or 44-day-old inoculum (table 1). The differences were least marked at 25° C in the solutions supplemented with thiamine and pyridoxine, and most marked in the solutions supplemented with thiamine only. This suggests that as an excised root grows in a thiamine solution, it slowly accumulates something which favors later growth of its fragments when they are transferred. This material did not reach its maximum in 14 days. However, pyridoxine was beneficial no matter whether the inoculum was 14 days old or 44 days old.

**Roots Grown in Medium Supplemented with Thiazole.** We reported earlier<sup>3</sup> that at times it was difficult to maintain roots in a solution supplemented with thiazole only, though we have grown excised tomato roots for 105 successive passages in a solution of mineral salts, cane sugar, and thiazole. Beginning with the 116th passage (96th successive passage in the thiazole solution), increasing difficulty was experienced. From the 120th to 126th passage, the roots grew very slowly reaching an average weight of about 3.0 mg. even after 4–6 months growth. This compares with 6–16 mg. in 2 months during the 84th to the 96th passage (1). The slowness of growth was not due to any error in the preparation of the basal nutrient solution because the series in the same basal solution supplemented with thiamine grew satisfactorily. We suspected the possibility that the stock thiazole might have decomposed but tests with *Mucor Ramannianus* showed the thiazole to be functional. We concluded that the roots themselves in their long cultivation had become modified and were less able to grow in the Pfeffer's solution supplemented with thiazole than they were originally.

We considered that these roots might have lost the ability to synthesize pyrimidine. However, when roots which had been continuously cultivated in solutions supplemented with thiazole were transferred to solutions containing thiamine, little improvement in growth occurred although three successive transfers were made in the thiamine solution.

#### SUMMARY

The strain of excised tomato roots which has been maintained for 144 passages, each approximately 1 month in length, grew slowly at 15° and more rapidly at 20° or 25° C; 25° C was somewhat superior to 20° C.

<sup>3</sup> Robbins, William J. A report on the growth of excised tomato roots. Jour. Arnold Arb. 27: 480–485. 1946.



The roots could not be maintained at 30° C. Pyridoxine was beneficial in the presence of thiamine at all three temperatures. Excised roots which had grown 14, 32, and 44 days in a particular passage were used as inoculum. Pyridoxine was beneficial for all three types though consistently lower dry weights were obtained with the youngest inoculum. Roots which had been grown for 96 successive passages in a solution supplemented with thiazole proved difficult to maintain. Some change in their metabolism apparently took place which made them difficult to cultivate in solutions supplemented with thiazole or thiamine.

DEPARTMENT OF BOTANY, COLUMBIA UNIVERSITY

AND

THE NEW YORK BOTANICAL GARDEN

NEW YORK

## TORREYA

## PROCEEDINGS OF THE CLUB

**Minutes of the Meeting of April 6, 1948.** The meeting was called to order by President Small at 8:05 P.M. at Columbia University; 75 members and friends were present. The minutes of the preceding meeting were read and approved. Dr. Barbara McClintock of the Carnegie Institution of Washington, Cold Spring Harbor, New York, spoke on "The relation of a gene-controlled breakage of a chromosome to the general problem of genic instability."

The meeting was adjourned at 9:40 P.M.

**Minutes of the Meeting of April 21, 1948.** The meeting, at Hunter College, was called to order by President Small at 8:40 P.M.; 25 members and friends were present. The minutes of the preceding meeting were read and approved. Dr. M. A. Johnson, of Rutgers University, spoke on "The Shoot Apex in Vascular Plants." His abstract follows:

The structure and organization of the shoot apex in vascular plants was described and compared. The apex in the lower forms is either dominated by a master apical cell or by a group of initials which contribute to the tissues of the shoot. Both conditions may occur in a single genus, as in *Selaginella*. The cycads have an apical, superficial, initiating layer but their apices are noteworthy for their striking zonation; two prominent features are a central region of mother-cells and an active, flanking, meristematic mantle. In the higher gymnosperms the apices are not only smaller but fail to show the degree of zonation seen in the cycads. Periclinal divisions are less frequent in the superficial layer, especially at the tip of the apex. They appear to be entirely absent both at the tip and in the flanks of the apex of *Gnetum* except during leaf initiation. The angiosperms possess apices with two rather distinct zones; an outer consisting of one or more layers of cells—the tunica—which increases in area, and an inner core—the corpus—which increases in volume. The problems in deriving the angiosperm shoot apex from the gymnospermous types were discussed. Further evidence is required before more than tentative conclusions can be reached. It is possible, however, to arrange a more complete intergrading series between the gymnospermous and angiospermous types of shoot apex than was formerly supposed to exist.

The meeting was adjourned at 9:50 P.M. Refreshments were afterwards served in the laboratory by the Hunter College department of botany.

**Minutes of the Meeting of October 20, 1948.** The meeting was called to order at Columbia University by President Small at 8:15 P.M.; 24 members and friends were present. Dr. P. P. Pirone of The New York Botanical Garden gave an illustrated discussion of "Some Important Diseases of Shade Trees." His abstract follows:

Shade trees, like all living things, are subject to several highly destructive fungus and virus diseases. Perhaps the most important fungus disease in the present century, which was largely responsible for making the public "tree conscious," is the chestnut blight.

Another, though perhaps not so destructive one, is the Dutch elm disease which has destroyed thousands of fine elms in the northeastern United States in the past fifteen years.

Of more recent origin, and more destructive than either of the two, is the virus disease of American elm known as phloem necrosis. Thousands of large elms in Columbus, Ohio, alone have succumbed to this disease in the last few years. One vector for this disease has recently been determined as the leafhopper *Scaphoideus luteolus*. Tests are now under way to determine whether DDT applications will control the leafhopper and thus check the spread of the disease.

The London plane (*Platanus acerifolia*), often incorrectly referred to by nurserymen as the Oriental plane, is subject to several highly destructive fungus diseases.

The first is cankerstain, first found near Philadelphia and now occurring over a wide area, which is highly fatal. Infection usually occurs through man-made wounds. Spread from diseased to healthy trees also occurs through use of contaminated pruning saws, poles, and other arborist's equipment.

Apparently new to science is the *Dothiorella* canker disease, still largely confined to the metropolitan New York area. Nearly fifty confirmed cases have been found within the past year and all have been disposed of by burning to check further spread.

The minutes of the preceding meeting were read and approved. The meeting was adjourned at 9: 15.

**Minutes of the Meeting of November 17, 1948.** The meeting was called to order at 8: 05 P.M. by President Small at Hunter College; 42 members and friends were present. Dr. Michael Levine, of Montefiore Hospital, spoke on "Growth and Differentiation of Plant Tissues in vitro." His abstract of the address follows:

Intercalary meristem of the tap root of *Daucus carota*, and of stems of *Helianthus annuus*, *Nicotiana Langsdorffii*, *N. affinis*, *N. tabacum*, *N. glauca*, and *N. glutinosa*, was grown aseptically on synthetic media to which 0.6 per cent of well mashed shredded agar-agar was added. Growth of these tissues was increased by the addition of 0.5 mg. per cent of indole acetic acid or less of  $\alpha$ -naphthalene acetic acid. The chemical carcinogens, 1,2,5,6-dibenzanthracene, 3,4-benzpyrene, or 20-methycholanthrene, were added in varying concentrations to the media to determine the effect of these agents on these tissues. The meristem of the carrot root gave rise to three types of tissue masses. The nodular tissue mass was characterized by pigmented globular masses from which there occasionally appeared a sparse distribution of roots. The whole mass assumed an inverted cup-shaped form and in a medium with one of the growth substances or a chemical carcinogen this tissue in section presented the appearance of crown gall, "plant cancer." Cultures of the thalloid form were pale green in color and consisted of thallus-like bodies, broad-tipped and tapering at the base. These bodies were composed of parenchymatous tissue with irregular strands of vascular elements. Under the influence of the chemical carcinogens the epidermal cells in these organized bodies proliferated and formed numerous buds of embryonal tissue. These differentiated and formed abortive and normal plantlets.

The hyaline or third type of tissue mass was the most common form following the use of heteroauxin. It was yellowish-brown in color and produced an abundance of roots. This tissue mass transferred to media with one of the carcinogens or a standard substrate produced completely differentiated plantlets typical of the carrot. Roots and leaves of these cultures grown on low concentrations of indole acetic acid de-differentiated and formed hyaline tissue masses.

Segments of stems of *N. Langsdorffii* and *N. affinis* formed tissue masses in consistency not unlike those of the hyaline tissue masses of the carrot. Fully differentiated plantlets have grown from these tissues. Stem segments of *N. tabacum* produced surface proliferation and formed buds from the meristem which developed stems, leaves, and finally roots. These reactions are unlike those in the carrot.

The factor responsible for the differentiation of the tissue masses into complete plantlets are not conclusively established. Indole acetic acid in culture media facilitates growth, induces changes in tissue organization; roots are formed. Its influence on differentiation of stem tissue may be indirect. The chemical carcinogens used in these experiments produce malignant growth in animals. In these studies evidence of growth, stimulation, hyperplasia, bud formation, and complete differentiation occur in their presence. Factors needed to convert normal cells into malignant growths seem to be lacking in the plant.

The meeting was adjourned at 9:15 for refreshments served by the Hunter College botanists.

**Minutes of the meeting of December 2, 1948.** The meeting was called to order at 8:15 P.M. by President Small at Hunter College; 50 members and friends were present. Dr. Rudolf Florin of the Hortus Bergianus, Stockholm, spoke on "The Telome theory in its Application to the Reproductive Organs of the Cordaites, Conifers, and Taxads." His summary follows.

According to the telome theory (W. Zimmerman 1930, 1938, 1945) the transformation of the simple organization of the earliest vascular land plants of the Upper Silurian and the Lower and Middle Devonian formations into the more complicated organization of the geologically younger tracheophytes, including those of the present time, is the result of a few principal organogenetic processes running their course more or less independently, viz. overtopping, planation, fusion, reduction and recurvation. The overtopping of a uniform truss of dichotomizing telomes (and mesomes) leads to its differentiation into an axis and lateral organs, the latter with a primary alternate arrangement. The planation implies a change of the primary cruciate dichotomy into flabellate dichotomy, i.e. the telomes (and mesomes) are brought into the same plane. The fusion connects telomes (and mesomes) either by parenchyma alone ("webbing") or, in addition, by the steles of the telomes (and mesomes). The various types of steles have arisen by fusion from the protostelic condition of the earliest vascular plants. Reduction of an overtopped telome system may ultimately lead to the formation of a simple uninerved leaf. Recurvation of telomes occurs particularly in fertile organs.

The telome theory is of interest in connection with the problem of the evolution of the reproductive organs in the cordaites, conifers, and taxads. The radial, repeatedly dichotomized sporangial trusses of the earliest vascular plants—with terminal erect sporangia—are a primitive type from which, according to this theory, all sporangial trusses of the tracheophytes derive. There is a large gap between this primitive condition and that represented by the organization of the Upper Carboniferous cordaites, which have radially symmetrical fertile dwarf-shoots or flowers arranged in inflorescences and constituting much transformed lateral mixed telome systems. The female flower is composed of an axis carrying spirally disposed

bifurcated leaves (telome trusses) or simple leaves (telomes), and ovule-bearing megasporophylls (sporangial trusses). But these axillary, partly fertile dwarf-shoots of the cordaites have retained primitive features, such as the radial symmetry, the spiral arrangement and dichotomous branching of the leaves and megasporophylls, and the terminal position of the sporangia. At the apices of the megasporophylls the mesomes became aggregated, so that three telomes arose from the same point of furcation: two lateral vegetative telomes forming the integument and one terminal fertile telome (sporangium).

The more reduced of the two cordaites types of female flowers known so far leads directly to the *Lebachia* type of the earliest conifers from the Upper Carboniferous and Lower Permian formations. The megasporophyll of *Lebachia* with its single, terminal, erect ovule entirely corresponds to that of the later cordaites and may therefore also be assumed to derive from a dichotomized truss of terminal naked sporangia. The integument has the same nature as in the cordaites.

In the conifers the sporophylls and sterile scales on the axis of the female flower soon changed from the primitive spiral to a decussate arrangement by rhythmically repeated reduction of mesomes. Further, the anterior part of the flower was suppressed, and the sporophyll became strongly reduced and incorporated in the sterile part of the flower, so that finally the ovule appears to be seated directly on the surface of this so-called ovuliferous scale.

The female flowers of the taxads differ from those of the true conifers by not being arranged in inflorescences and by the absence of lateral fertile telome systems on the floral axis. The uppermost of the overtopping branches of the whole primary telome system, from which the flower derives, was a fertile telome or sporangium. Consequently this became placed terminally on the floral axis itself. The integument appears to be formed out of two or more vegetative aggregated telomes—or in certain cases, telome systems—which constitute overtopping lateral branches of the floral axis. In position, each of these telomes or telome systems corresponds to a whole sporangial truss (megasporophyll with several ovules or, after reduction, one single ovule) in the cordaites and conifers.

While the structure of the female cones of *Lebachia* apparently derives from that of the inflorescences of the cordaites, their male flowers differ considerably. In the earliest conifers, the floral axis carries exclusively microsporophylls in its fertile region, which are moreover hypopeltate, hyposporangiate, and bisporangiate, while in the cordaites the microsporophylls are intermingled with sterile scales and terminated by clusters of 4-6 erect sporangia. In the earliest conifers, the male flowers are placed singly and terminally on branchlets, while in the cordaites they are united into inflorescences. The primitive nature of the cordaites microsporophyll is evident from its branching by cruciate, isotomic dichotomy. It derives from an undifferentiated telome system with terminal sporangia, which was subjected to reduction of its upper mesomes and to flattening of the basal mesome, so that the microsporangia became seated at the tip of a uninerved sporophyll, just as the ovule is.

The microsporophylls of the conifers and taxads represent more advanced stages than those of the cordaites. The taxads have radially sym-

metrical or dorsiventral microsporophylls, in one genus intermingled with sterile scales. The peltate, perisporangiate microsporophyll of *Taxus* appears to be the more primitive in this group and to derive from a dichotomized telome system with terminal erect sporangia. This conception implies the assumption that the peltate, perisporangiate organization is a transitional stage in the course of the organogenetic development, which led to the confinement of the sporangia to the abaxial side of the sporophyll. In the later true conifers, as in *Lebachia*, the axis of the male flower always carries exclusively sporophylls in the fertile region; these are moreover dorsiventral, hyposporangiate, and hisporangiate to plurisporangiate. They probably also derive from radial, undifferentiated, and dichotomizing sporangial trusses, with terminal erect sporangia. The conifers differ from the taxads, however, in that the peltate, perisporangiate stage in the organogenetic development of the microsporophyll seems to have been absent.

After extended discussion, the meeting was adjourned at 10:20. No business was transacted. Refreshments were served by the staff of Hunter College.

**Minutes of the Annual Meeting, January 5, 1949.** After dinner at Hunter College the annual meeting was called to order by President Small at 8:10 P.M.; 76 members and friends were present.

The minutes of the four preceding meetings (at which no business was transacted except for the reading of papers) were read in summary and approved.

The following were elected to membership in the Club: Honorary Life Member: George T. Hastings, Santa Monica, Calif. Active Members: Don S. Bolley, Brooklyn, N. Y.; Richard S. Cowan, New York, N. Y.; Albert W. Cross, Palo Alto, Calif.; Samuel J. Golub, Springfield, Mass.; Seymour Hutner, New York, N. Y.; Ivar Jorstad, Oslo, Norway; Pauline F. Kayser, Brooklyn, N. Y.; Edwin B. Kurtz, Jr., Tucson, Ariz.; Irwin E. Lane, Honolulu, Hawaii; Barbara McClintock, Cold Spring Harbour, N. Y.; Robert B. Platt, Emory University, Ga.; Richard A. Popham, Columbus, Ohio; Harry Thiers, College Station, Tex.; Associate Members: Augusta Allen, Allenwood, N. J.; Louis Lichtenberg, Newark, N. J. Three resignations were received with regret.

Mr. Vernon L. Frazee was appointed chairman of the Field Committee.

Dr. Simpson reported on the activities of the Program Committee, announcing the discontinuance of the afternoon meetings and adoption of the practice of holding two evening meetings a month. As chairman of the Exchange Committee Dr. Simpson reported that the Bulletin is at present exchanged for 22 publications.

Dr. Lawton gave a preliminary Treasurer's report which included the information that income for the past year had exceeded both estimates and expenditures by about \$500; that \$2,700 was available from past surpluses for the publication of the seventy-five-year Index of the Bulletin; and that the endowment fund amounted to somewhat more than \$26,500; that the club had 731 members of whom about 540 were Active Members; and that there were about 300 paying subscribers to the Bulletin. The President announced that Mr. Peloubet and Dr. Hammond would serve as Auditing Committee.

Dr. Camp presented for Dr. Rickett the report of the editor of the Bulletin. It was pointed out that Volume 75 included 750 pages, and this unusual size was made possible by the subsidization of 115 pages; that the number of articles submitted was increasing, to the point where it may be difficult to have publication keep pace with the authors; that the cost of publication is approaching \$10 a page (compared to \$5.25 in 1940); and that studies had been undertaken of more economical means of publication. Dr. Camp reported also that 74 of the 75 published volumes of the Bulletin had been indexed.

Dr. Matzke reported on his duties as delegate to the New York Academy of Sciences and for the Andrews Fund Committee, and Dr. Small for the Local Flora Committee.

Dr. Clum, as Business Manager, reported a net income from back numbers of the Bulletin, the Memoirs, the Index, and *Torreya*, and from advertising in the Bulletin, of \$1213.38.

Dr. Levine reported on the activities of the Membership Committee.

Dr. Seaver's report for the Budget Committee consisted of the following: Estimated Income—\$7500.00; Estimated expenses—Bulletin publication, \$5500.00; Advertising \$275.00; *Torreya* reprints, \$150.00; Index cards, \$275.00; Bibliographer's honorarium, \$150.00; Treasurer's office, \$200.00; Treasurer's honorarium, \$150.00; Business Manager, \$200.00; Corresponding Secretary's office, \$125.00; Recording Secretary's office, \$25.00; Editor's office, \$50.00; Membership committee, \$150.00; Field Committee, \$200.00; General expenses, \$50.00; Total, \$7,500.00. It was moved, seconded, and carried without dissent that this budget be adopted for 1949.

Dr. Small reported, as delegate to the New York and New Jersey Trail Conference, on the preparation of a guide-book to the local segment of the Appalachian Trail. He also gave an account of a meeting concerning the destruction of the swamp in Van Cortland Park, and the proposed formation of a Conservation Council of Greater New York. It was moved, seconded, and carried without dissent that a committee be appointed to formulate a resolution protesting the transforming of the swamp into a part of a golf-course. It was also moved, seconded, and carried without dissent that the Club participate in the proposed Council, there being no appropriation authorized by this action.

Dr. Simpson reported, for the tellers, that the mail ballots had selected the following officers for the Club: President, Edwin B. Matzke; 1st Vice-president, Charles A. Burger; 2nd Vice-president, Marion A. Johnson; Corresponding Secretary, Jennie L. S. Simpson; Recording Secretary, Donald P. Rogers; Treasurer, Elva Lawton; Editor, Harold W. Rickett; Business Manager, Harold H. Clum; Bibliographer, Lazella Schwarten; Representative on Board, N. Y. Botanical Garden, Rutherford Platt; Delegate, N. Y. Academy of Science, Michael Levine; Representatives, A.A.A.S., P. W. Zimmerman, Ralph H. Cheney; Members of the Council, L. M. Black, P. P. Pirone, Norma E. Pfeiffer, George S. Avery.

It was moved that the nominations be closed and the Secretary directed to cast one ballot for the persons named; the motion was seconded and carried without dissent, and the officers declared elected.

After the business meeting, which adjourned at 9:10, Dr. Small gave his address as retiring President on the activities of the Field Committee for the past ten years; his account was illustrated with colored slides, made on various field trips of the Club.

Respectfully submitted,

DONALD P. ROGERS,

Recording Secretary

## NOTES

Two new biological periodicals deserve mention. *Hydrobiologia*, subtitled *Acta hydrobiologica, limnologica et protistologica*, is published at The Hague. The first issue reached New York in October, 1948. It contains articles on dangerous algae from the United States and from South Africa, on phytoplankton of the Mediterranean, on photosynthesis in the phytoplankton, besides several taxonomic papers. Authors are from Michigan, Cape Town, Barcelona, Switzerland, Holland, Budapest, Praha, and Zagreb. The table of contents is followed by the titles announced for the next issue, with a similar international group of authors.

*Vegetatio*, subtitled *Acta geobotanica*, also published in The Hague, is the official

organ of the Association Internationale de Phytosociologie. It also includes papers in a variety of languages, by botanists of France, Switzerland, Holland, Spain, and Palestine.

Such evidence of international cooperation in science is encouraging, and it is to be hoped that these publications will have an enthusiastic reception.

## REVIEW

**The Evolution of *Gossypium* and the Differentiation of the Cultivated Cottons.** By J. B. Hutchinson, R. A. Silow and S. G. Stephens. i-xi, 1-160, f. 1-10 + pl. 1-9. London: The Oxford University Press. 1947.

With the closing of the Genetics Department, Cotton Research Station, Trinidad, B.W.I., a notable era in the advancement of cotton research was terminated. We are indebted to Hutchinson, Silow and Stephens for combining the results achieved by the investigators at the Cotton Research Station with the work of Harland in Peru, and of Beasley, Kearney and Webber in this country, into an extremely interesting and lucid description of the evolution of the cotton plant.

The book is divided into four parts. Part One, "The classification of the genus *Gossypium*," is by Hutchinson; Part Two, "The evolution of the species of *Gossypium*," is by Hutchinson and Stephens; Part Three, "The differentiation of the true cottons," is by Hutchinson and Silow; and Part Four, "The significance of *Gossypium* in evolutionary studies," is by Hutchinson and Stephens. These separate parts are not a series of disconnected essays as one might expect, but a well-digested account of the factors contributing to the evolution of a genus, unique by the fact of its long historical association with man.

There is general agreement among cotton investigators in regard to the main facts that emerge from this work.

1. The species of *Gossypium* may be conveniently segregated into three groups: (a) the wild species ( $n = 13$  chromosomes) found in both Old and New Worlds; (b) the Old World cultivated cottons ( $n = 13$ ); (c) the New World cultivated cottons ( $n = 26$ ). An important exception is the Hawaiian tetraploid cotton, *G. tomentosum* Nutt. It appears to be a truly wild species, and genetically it is closely related to the New World cultivated cottons.

2. Independent genetic and cytological evidence indicates that the New World cultivated cottons are allotetraploids with one genome homologous with that of the Old World cultivated cottons, while the other genome is homologous with that of the wild American species. Evidence derived from experimentally produced allopolyploids points to the probability that the Old World cultivated ancestor was *Gossypium arboreum* L., or a close relative. The nearest living ancestor of the American wild species appears to be *G. raimondii* Ulb., a wild species from the coast of Peru.

3. The wild, lintless species of *Gossypium* have a wide geographic distribution in the tropics and subtropics of both hemispheres. This is not true of the individual species, which for the most part are narrowly restricted in distribution. They are xerophytic, perennial shrubs, genetically well separated, and of low intraspecific variability. According to the authors, "Judging from the wild species, *Gossypium* is a stationary or receding genus made up for the most part of ancient relic species."

4. On the other hand, the cultivated cottons are an aggressive group. As a result of their close association with man, they have found congenial habitats within a wide belt of the earth's surface in tropical and subtropical lands. This success is evidently based on two characters, namely, the convoluted lint hairs, and the annual habit. Each character is comparatively simple genetically but the change (i.e. from lintless to linted) has involved the entire reorganization of the genotype, through the accumulation of gene differences.

The chief area of controversy concerns the time at which the American cultivated allotetraploids originated. Harland has suggested that the ancestral species were brought together over a Pacific land bridge in late Cretaceous or Tertiary times. The present authors have developed a number of serious objections to this theory that appear to make it untenable.



Recently Stebbins<sup>1</sup> has advanced a suggestion that does away with the necessity of the Pacific land bridge portion of Harland's theory. He assumes that hybridization between the parental genomes occurred in North America, probably during the early part of the Tertiary period. From this center the allopolyploids spread southward, as well as out into the Pacific Islands. "With the cooling of the climate in the middle of the Tertiary period, all except certain of the New World diploids disappeared from North America, but the tetraploids survived in South America and perhaps also on the West Indies." This proposal clears away some of the objections to Harland's theory, but certainly not all of them.

Hutchinson and Stephens, in contrast to Harland, believe that the New World allotetraploids are of comparatively recent origin. They suggest that the Asiatic cultivated cottons were carried by an ancient civilization across the Pacific, to the mountain valleys of northwestern South America, where natural hybridization of the cultivated crop with a neighboring wild species (presumably *Gossypium raimondii*) produced the first allotetraploid. There are a number of pieces of evidence, biological, ethnological, and archaeological, which when fitted together form a rather consistent picture in favor of the theory of recent origin. However, none of the evidence, if considered independently, is decisive. The chief stumbling block is the negative and highly speculative nature of the argument for the crossing of the Pacific from Polynesia to South America by an ancient culture.

In their zeal to support the recent origin theory by trans-Pacific migration the authors are guilty of a minor error. They have listed *Cucurbita* as having two Old World centers of origin. *Cucurbita* is strictly a New World genus; there is not the slightest evidence of any species being endemic in the Old World.

Students of evolution will be interested in the stimulating discussion of the development of new characters and the significance of polyploidy. The chapter on the evolutionary prospects of a crop plant will be illuminating to those whose studies have been confined to non-domesticated species.

The quality of the paper, the printing, and binding are exceptionally good for these times. The photographs, line drawings, and maps are well reproduced. There is a list of approximately 160 references, and three separate indexes (I, Index of names of species, varieties and races of *Gossypium*; II, Index of authorities quoted; III, General index).

Finally, in planning research with crop plants, administrators of agricultural programs in this country might well follow the example set by the far-sighted policy of the Empire Cotton Growing Corporation. This little book of 160 pages is proof of the wisdom of including fundamental botanical and genetic studies in a crop research program.—THOMAS W. WHITAKER.

<sup>1</sup> Stebbins, G. L., Jr. Evidence on rates of evolution from the distribution of existing and fossil plant species. Ecol. Monogr. 17: 149-158. 1947.

# INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LIAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITOR OF THE TAXONOMIC INDEX

## TAXONOMY, PHYLOGENY AND FLORISTICS

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(See also under Phytopathology: **Allington: Gorenz, Walker & Larson**)

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RETICULOMYXA FILOSA GEN. ET SP. NOV.,  
A NEW PRIMITIVE PLASMODIUM

RUTH N. NAUSS

In a field collection made in the metropolitan area of New York City during the summer of 1937, a remarkable versatile plasmodium was found. It has characters of both plants and animals, but no botanists or zoologists consulted, including the late Professor R. A. Harper, had seen any form resembling this extraordinary plasmodium. A report of its discovery has been withheld (1) in the hope that its possible mode of reproduction other than by fission could be definitely determined, which has not yet been possible, and (2) that the literature could be searched more thoroughly, an opportunity for which was made available last year.

The new plasmodium appears to resemble very closely several species of *Proteomyxa* that were discovered in the latter half of the 19th century. The descriptions of these are often incomplete and even sometimes rather obscure. Because so little is seemingly known about such primitive organisms today, a somewhat detailed comparison of the early species with the new plasmodium will be made in a separate paper, the present one being confined to a description of the new organism and to a few characters it has in common with certain other forms, especially the *Myxomycetes* and the *Foraminifera*.

The discoverers of the proteomyxan species that closely resemble the new form gave each a different generic name, although it seems possible that some of them may belong to a single genus. Because of this and the incompleteness of some of the descriptions, owing to limited observation, I feel that it is necessary to regard the new plasmodium also as a new genus, for under varying circumstances and conditions it has revealed characters and habits apparently not recorded for the earlier forms. In recognition of one of its outstanding characters, namely the unusual abundance of the anastomosing, filose pseudopodia, I therefore propose for this new organism the name *Reticulomyxa filosa*, suggested by Dr. Libbie H. Hyman.

*Reticulomyxa* Nauss, gen. nov. Plasmodium nudum, multinucleatum, semper proteum, tunicam qualemcumque carens, ex areola centrali plasmatica continua compositum et reticulo peripherico, e pseudopodiis filiformibus anastomosantibus longissimis, unaque orientibus, complecto; plasmatis fluentia peripherica et centralia semper opposita; vacuola numerosa haud contractilia; plasma creberrime granulosa, nec in ecto- et endoplasma discrimen patiens.



Naked, multinucleate plasmodium of everchanging shape. No wall or other permanently formed enveloping membrane. Central protoplasmic area surrounded by an intricate network of very long, active, anastomosing filose pseudopodia, which arise from any point on the surface. Pseudopodia possessing a simultaneous two-way or sleeve-type of flow: out through the center, back on the periphery. Many noncontractile vacuoles while vegetating, cytoplasm thickly granular, no differentiation into ecto- and endoplasm.

*Reticulomyxa filosa* Nauss, sp. nov. Plasmodium aquaticum vel semiaquaticum, album vel roseolum, in cultura semiaquatica in tumulos minutos contractum, aquatica in lamellam latam extensum, areola centrali ad 4 mm. (6 mm. maxime extensa) diam., fere immobili, canaliculis in quibus gluenta alterne opposita notata, pseudopodiis longitudinem decemplex attingentibus, interdum crassitudines fusiformes areolasque alveolares exhibentibus, maturiora interdum cuncta migratoria, in plasmodia pauca (pro usu tria) fissa, vel in aquam novam translata in corpuscula sporoidea diffracta.

Plasmodium aquatic and semiaquatic, white, rarely shell pink. In semiaquatic cultures concentrated in small heaps, in aquatic often extended in a broad sheet, the central plasmodial area measuring to 4 mm. in diameter (6 mm. when fully extended), almost immobile, with many parallel channels in which the flows are alternately opposed; the pseudopodia attaining a length of ten times the central area, occasionally exhibiting fusiform thickenings and small alveolar areas; mature plasmodium homogeneously finely granular, periodically migrates to new site and divides longitudinally into daughter plasmodia (usually 3), disperses spore-like bodies when transferred to fresh dish of water.

**Materials and Methods.** The plasmodium of *R. filosa*, which has been in continuous cultivation since it was first found, was originally seen in a culture of slime-mold plasmodia which was started from decaying leaves on moist blotting paper. The leaves were collected in the woods in a depressed, soggy area, about five feet in diameter, that lies close to the edge of a tidal swamp. The ground is kept moist by a trickling stream from a spring, and old leaves and other vegetation fall here year after year. Since its discovery, *R. filosa* has been taken from this area several times along with slime-mold plasmodia, once even during a warm spell in January. It is not abundant nor is it found in every collection. This species was also obtained with slime molds about two miles distant from the spring, where its substratum was a damp, rotting ground log, since destroyed in drainage work. No sphagnum has been seen in or around these collecting areas.

*R. filosa*, together with its associated slime molds, was isolated by the same method as that used for *Hemitrichia vesparium* (Batsch) Macbr. and other species (Nauss 1943, 1947): moist, decaying vegetation was placed on white blotting paper in petri dishes, and kept supersaturated with tap water. Later it was found that it could be secured readily simply by

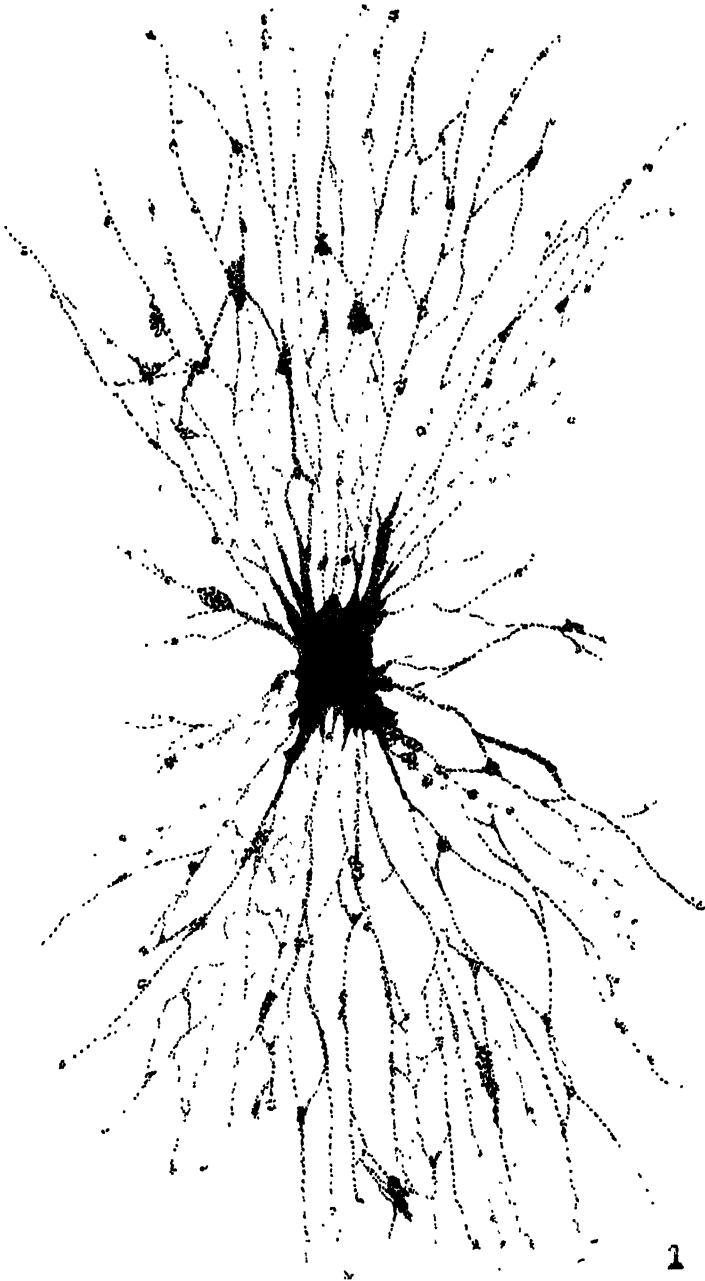


FIG. 1. Young, vegetating plasmodium, with anastomosing, filose pseudopodia; as seen in aquatic cultures. Granular masses of protoplasm scattered throughout pseudopodia. Approximately  $\times 8$ .

placing the selected material in a dish of water. *R. filosa* thrives best on pulverized wheat germ, which is sifted lightly on the cultures every day or so except when it is maturing. When the species is grown with certain slime-mold plasmodia, the pulverized rolled oats fed to them seems sufficient to keep *R. filosa* flourishing for long periods of time. Cultures are grown at room temperature and transferred about once a week.

Stock cultures are maintained by placing in a petri dish a disc of blotting paper that has been cut from the center into eight equal wedge-shaped sections, saturating with water, inoculating with plasmodia, and supplying with suitable nutrient periodically. When a culture is thriving, four of the best sections bearing plasmodia are transferred to a clean dish with four new, similarly shaped sections of paper inserted alternately between them so as to cover the bottom. Water and nutrient are then added. Jars are also used for stock cultures. They are filled with about an inch of water and lined to the bottom with 2-inch squares of blotting paper. A few plasmodia are transferred with small tweezers to the water-line, where they eventually grow and spread laterally around the jar.

A satisfactory method for studying this plasmodium is to place a petri dish, partially filled with water, on the stage of the microscope and transfer to it a plasmodium with a portion of its blotting paper substratum. After a day or so the entire plasmodium will leave the paper and creep out into the water, where it can be observed for hours at a time with a water-immersion lens without fear of undue evaporation. Jarring of the culture usually disturbs this delicate plasmodium. The use of vital stains has been helpful in studying it in the living state. For critical cytological study, plasmodia are stained in situ with Heidenhain's iron-alum haematoxylin.

The accompanying photomicrographs show only a few of the seemingly endless varieties of form that *R. filosa* is capable of assuming. Most of those included have been observed often. Since the pseudopodia and the main body of the plasmodium frequently grow at different levels, it is usually difficult to get both in focus at the same time. Hence, the apparent absence of pseudopodia in figures 2 and 7.

The general features of protoplasmic streaming of *R. filosa* have been filmed successfully by Dr. William Seifriz, the organism having been made available to him on several occasions at his request.

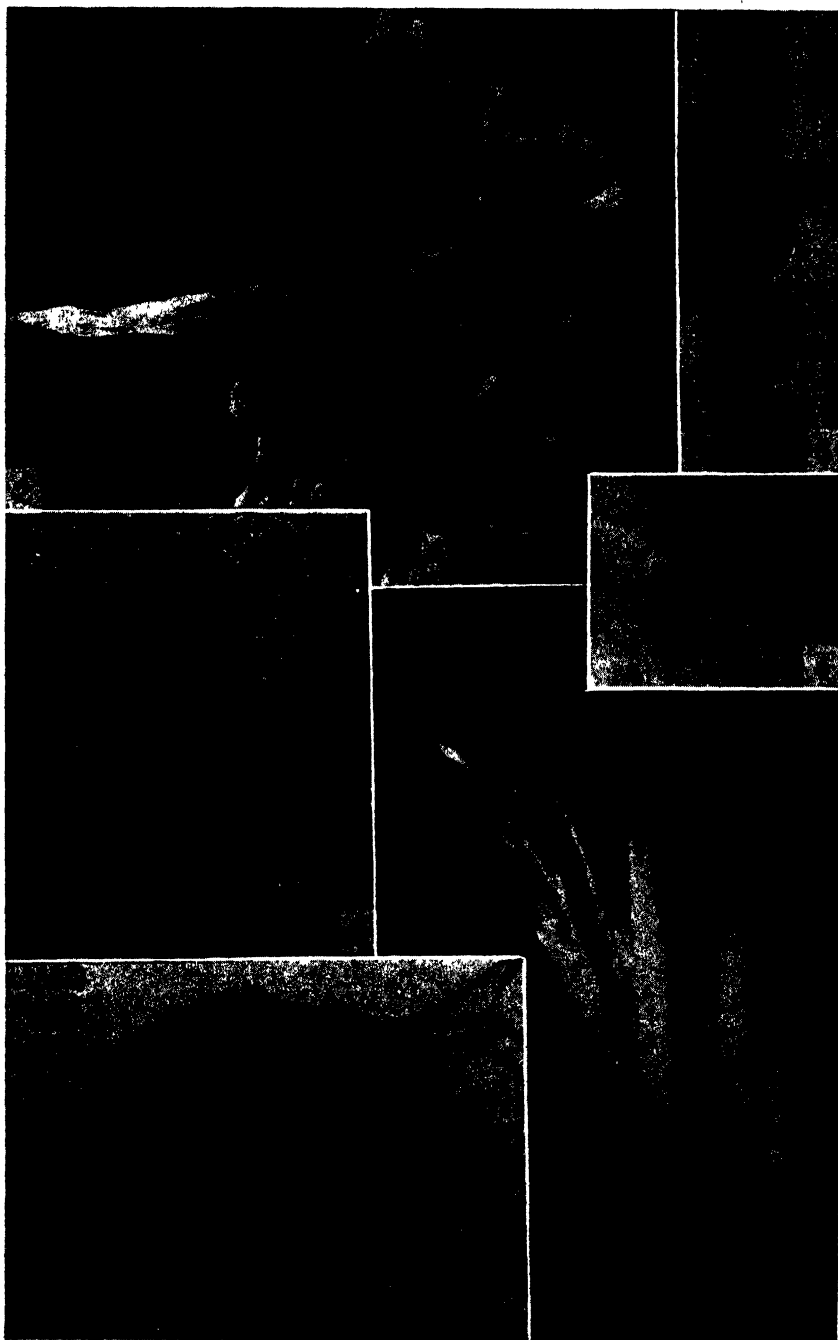
**Description and Habit of the Plasmodium.** The plasmodium of *R. filosa* is a multinucleate mass of naked protoplasm that appears to be devoid of significant structure (fig. 1). It is continually changing shape, being without a shell or other permanently formed membrane. The cytoplasm is thickly granular and in the vegetative stage contains an unusu-

ally large number of noncontractile vacuoles. Portions of protoplasm that become detached continue to develop. In all these respects *R. filosa* resembles the plasmodia of slime molds, except that the latter generally have fewer vacuoles. Unlike them, however, *R. filosa* has a central body portion that remains fairly stationary during vegetation, gathering its food by means of a highly organized system of anastomosing, filose pseudopodia that arise from any point on its surface and have a concurrent two-way flow. There is no apparent differentiation into ectoplasm and endoplasm, so that granules and vacuoles circulate freely out into the pseudopodia.

The central portion measures up to 4 mm. in diameter, but when extended, up to 6 mm. These measurements do not include the long, anastomosing pseudopodia that often extend to as much as ten times the diameter of the central area in search of food. Many of them may cross over and under others without fusing (fig. 13), or a group of them may parallel each other in their meanderings, gracefully taking the curves as one. En masse these can be seen with the unaided eye as a narrow band of delicate white strands perhaps an inch in length, suggesting a row of telegraph wires. Under the microscope they are observed to be connected by an intricate network of smaller and more delicate pseudopodial threads (fig. 9), which in turn may be connected by still smaller ones. Such parallelism has also occasionally been noted in shorter, exceedingly delicate pseudopodia that enclose areas where spore-like bodies appear to be in process of liberation (fig. 12).

In addition to being aquatic, as the similar proteomyxan forms were, *R. filosa* also grows semiaquatically. Its appearance often differs in the two types of culture. In aquatic cultures the central area is a thin, sometimes long sheet of protoplasm that adheres to the bottom of the dish, the anastomosing pseudopodia radiating laterally. When grown semiaquatically, on moist blotting paper, the central area forms into a heap which rises above the surface of the paper, the pseudopodia not being visible. As many as forty to fifty such plasmodial heaps, varying in size, may be seen in a thriving 3-inch petri dish culture.

In a vegetating plasmodium the pseudopodia generally appear somewhat lumpy from particles of food they are carrying (fig. 1). It is rather uncanny to observe the most delicate strands gyratingly cabling-in chunks of food that are sometimes as much as six times their own diameter. If the load is too heavy, as when worms and rotifers have been captured, the task of hauling is shared by a number of them. This is always an amazing and fascinating process to watch, for the pseudopodia are continually anastomosing and pulling apart from one another all the way along till it



would seem the captured prey might never reach its destination. Not infrequently food appears to be partially digested in situ before being transported.

Some of the pseudopodia in fairly mature plasmodia do not seem to function as food-providers. These are usually larger and more in the nature of veins. At times a section of one will be composed of numerous fusiform or spindle-shaped bodies. In figure 8 the large diagonal vein (near top) gives some idea of their size and appearance, but they are frequently much more fusiform than these, with only a thin thread of protoplasm separating one from the other. A spindle may form at any point along large veins. As a rule, where one arises, others form in quick succession at the same point and then move on. Rhythmically the streaming protoplasm contracts at this point, each time pinching off and forming a new spindle. Thus a series of fusiform bodies comes into being. They glide along in tandem formation without incident until suddenly each in turn vanishes at a given point in the vein as rhythmically and as mysteriously as when first formed. These fusiform bodies are somewhat suggestive of those seen in species of *Labyrinthula* and *Chlamydomyxa* of the Proteomyxa, and also those observed occasionally in *Cribraria violacea* Rex of the Myxomycetes, a report on which is in preparation. In species of *Labyrinthula* and *Chlamydomyxa* they apparently glide along on filiform threads, often overtaking each other, whereas in *Cribraria violacea* they appear to remain stationary.

At times, instead of being fusiform or spindle-shaped, these bodies in *Reticulomyxa filosa* are globular and vary considerably in size for a given strand (fig. 8). Whether they represent a more advanced stage of the spindle form is not known. The globular forms appear to break down into smaller and smaller round ones that are finally abandoned by the thread of protoplasm that has carried them about (fig. 8, upper half). Their further development, which is very slow, has not yet been determined satisfactorily.

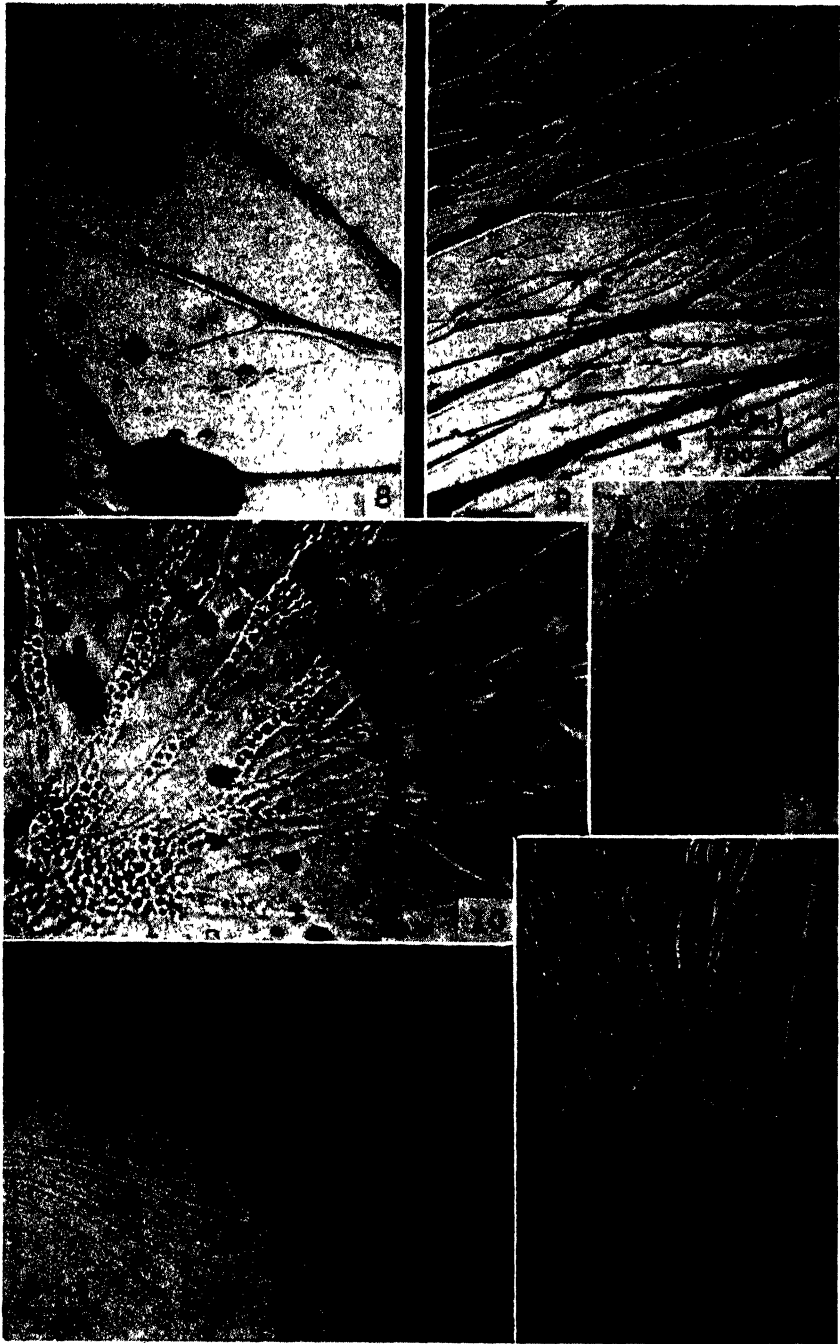
The plasmodium of *R. filosa* also has other significant features, one of which is the occasional alveolar character of the protoplasm. In figure 10

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#### Explanation of figures 2-7

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FIG. 2. Small plasmodium, as often seen on blotting paper cultures; anastomosing, filose pseudopodia not in focus. Approximately  $\times 50$ . FIG. 3. Apparent encystment under water as a result of lowered temperature.  $\times 200$ . FIG. 4. Young floating form, seemingly developed from spore-like bodies; two polar protoplasmic centers forming. Approximately  $\times 50$ . FIG. 5. Portion of a very small, mature floating plasmodium, with filose pseudopodia; stained with vital green. Approximately  $\times 200$ . FIG. 6. Structure apparently composed of exceedingly fine filose pseudopodia, lying at edge of plasmodium and attached to it by strong protoplasmic "guy" lines (see also figure 13); stained with eosin. Approximately  $\times 50$ . FIG. 7. Plasmodium dividing into three daughter plasmodia; long, anastomosing polar pseudopodia not in focus.  $\times 22$ .



protoplasm so characterized is seen emerging from the plasmodium and fanning out into the pseudopodia. Small sections of it then girate back and forth along the strands, finally being abandoned by the filose threads (fig. 11, lower right).

Another interesting form is that shown in figure 6, seemingly made up of exceedingly fine pseudopodia. These structures, which are observed only now and then, are somewhat variable in size and shape, and lie adjoining the plasmodium, as in figure 6, or at a short distance from it. In either case they retain a connection with the mother plasmodium. They later appear to form short, delicate nonanastomosing filopodia that wave freely about in the water, seeming to give off minute spore-like bodies similar to those in figure 12 mentioned earlier, which are too small to be seen clearly in the illustration. They also resemble those that appear when a mature plasmodium ruptures, described in the following paragraph. Further development of these spore-like bodies has been difficult to follow.

A mature plasmodium is waxy white in blotting paper cultures, its protoplasm being thick and opaque (fig. 5) and homogeneously finely granular. When such a specimen is transferred to a fresh dish of water, it bursts, dispersing minute spore-like bodies over the surface of the water and scattering large fragments of residual protoplasm that proceed to round up again and send out a few filose pseudopodia. After several days, young floating plasmodia are found (fig. 4), which are different in character from the residual protoplasm. Myers (1938) gives a somewhat similar picture of a marine species of Foraminifera, *Tretomphalus bulloides*, which has a test or shell. He states that when the asexual stage reaches maturity *T. bulloides* rises to the surface, where thousands of gametes are given off and that residual protoplasm continues to give rise to filose pseudopodia. Myers also says that although he has studied this species over a period of five years he has not been able to demonstrate development of the gametes beyond their union in fertilization. It is interesting to note that *Reticulomyxa filosa* further resembles the Foraminifera in possessing the same type of flow in the pseudopodia, the occasional pinkish tinge of the protoplasm, and in being multinucleate.

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#### Explanation of figures 8-13

FIGS. 8-13. A few of the varied patterns of pseudopodia and veins. FIG. 8. Globular and somewhat spindle-shaped bodies; small round ones (upper half) abandoned by protoplasmic threads. Approximately  $\times 200$ . FIG. 9. Parallel pseudopodia connected by finer protoplasmic meshwork. Approximately  $\times 100$ . FIG. 10. "Fan" pattern of alveolar protoplasm; stained with vital green. Approximately  $\times 1000$ . FIG. 11. "Triangle" patterns of alveolar protoplasm in pseudopodia; eosin stained. Approximately  $\times 200$ . FIG. 12. Curved pattern of parallel, filose pseudopodia enclosing meshwork of delicate anastomosing pseudopodia which appear to be liberating minute spore-like bodies too small to be clearly seen here. Approximately  $\times 50$ . FIG. 13. Enlarged area of protoplasmic guy lines of figure 6; eosin stained. Approximately  $\times 200$ .



The pseudopodial streaming in *R. filosa* is a simultaneous two-way or sleeve-type of flow: concurrently moving outward through the center and back on its wall or periphery, the protoplasm being more or less equally divided between the two streams. This type of flow, which is also common to a number of other organisms, is apparently present in the pseudopodia of *R. filosa* at all times. It is not so easily detected, however, in large veins of protoplasm that periodically carry the plasmodium to a new location, the process of which will be described later. At such times, the protoplasm seemingly appears to flow in one direction only, outward, with no return or peripheral flow taking place. Under very high magnification, though, even here the return flow has sometimes been observed, being scarcely more than a very thin film. In character this would seem to indicate that the strong urge to move outward is capable of almost obliterating the return flow, and possibly at times it virtually does.

Such is the picture of streaming in pseudopodia. That observed in the main or central part of a vegetating plasmodium is somewhat different. Here is a broad, thin sheet of protoplasm, consisting of many parallel channels of flow alternately opposed. As many as twelve have been counted in one very broad sheet. Streaming is continuous and rapid. The protoplasmic granules of one channel race very close by those of another. As no visible wall separates them, the result is nothing short of spectacular. Such wide bands of protoplasm with alternately opposed flow do not seem to have been described for similar organisms.

Movement never ceases. As the streaming protoplasm reaches the periphery of the central area, it often turns and finds its way back through some other channel. I have several times noted a somewhat comparable circulatory movement in the slime mold *Dictydium cancellatum* Macbr., which has been collected close to the spring where *R. filosa* was discovered. In small areas of this purple pigmented plasmodium the veins are divided longitudinally into two channels, the protoplasm in each flowing continuously in opposite directions, with no reversal of flow taking place. As in *R. filosa*, the protoplasmic granules of the two opposing currents move along quite closely to each other with no visible membrane separating them. Outside of such areas, however, the veins have only one channel of flow, the streaming manifesting the characteristic tidal flow of slime molds. I have not observed this unusual type of flow in any other species of Myxomycete thus far cultured, nor have I seen it reported in the literature.

The plasmodium of *R. filosa* has one outstanding habit, previously alluded to, namely, that of periodically moving off to a new location. Preparatory to this change of position, the filose pseudopodia are nearly

all withdrawn and the plasmodium appears to rid itself of all extraneous matter. This cleansing process is carried on by a kind of self-filtering or screening as the plasmodium begins to move forward to the new site. The result is a homogeneous, finely granular plasmodium and a discarded pattern or false body that is an exact replica of the departing plasmodium. This replica, being made up of excreted materials, is comparable in a way to the residue left as tracks by a slime mold, except that it is more in the nature of a cast of the entire departed plasmodial body than of the network of veins.

To transport itself to the new location, which may be as much as one inch away, the cleansed protoplasm of *R. filosa* flows through several large veins, which seemingly appear to move outward only. A short time after it begins to arrive at its destination it prepares for longitudinal division, which usually results in three daughter plasmodia of about equal size (fig. 7). This process of division, requiring from 8-12 hours to complete, begins anteriorly, the two outer daughters drawing away from the middle one at a slight tangent (fig. 7), so that by the time the last of the small connecting strands are severed, each daughter plasmodium is moving off in a divergent direction. Each creeps slowly about for a few days and then settles down to a more or less stationary existence, leaving to the energetic filose pseudopodia the task of finding and bringing in food. This habit of moving off and dividing does not seem to have been described for similar proteomyxan organisms.

Daughter plasmodia that have only recently become separated are elongated in shape and their filose pseudopodia are concentrated mainly at the anterior and posterior ends. These pseudopodia can scarcely be seen in figure 7 because they are growing at a different level from that of the plasmodial body. After several days, when a daughter plasmodium has settled down, it gradually becomes less extended and the pseudopodial threads begin to branch out gradually from other parts (figs. 1, 2), eventually forming the immense surrounding network that is so characteristic of this organism.

*R. filosa* seemingly does not withstand slow desiccation as most slime molds do. I have isolated two species of slime molds, however, that react as *R. filosa* does; they apparently cannot form viable sclerotium when slowly dried. These are the brown pigmented plasmodium of *Didymium nigripes* Fr., which is regularly found around the spring where *R. filosa* occurs, and an unidentified white plasmodium (Lab. No. 84), which was collected about fifty feet from this spring in 1939. Neither of these species seems to survive when dried after the manner of other Myxomycetes. They are therefore kept in the plasmodial stage only. *Didymium nigripes*

generally gives rise to sporangia within a few months after having been collected, while No. 84, which has been found only once, has never fruited in the laboratory. Unlike any other slime mold I have cultured, No. 84 thrives only when supplied with wheat germ, the optimum food of *R. filosa*. Whereas *R. filosa* requires food several times a week, however, No. 84 can be kept from 4-6 months on a single feeding.

On several occasions the new plasmodium has apparently encysted under water, as do some slime molds. Once during the winter when a culture of it was set on an inside window sill for a few days, the plasmodium broke up in situ along the veins (fig. 3) similarly to the unusual slime mold *Hemitrichia vesparium* (Nauss 1943). Also, when cultured several times along with algae, it has rounded up into small, irregularly shaped masses. Although both types of apparent encystment, on being restored to normal cultural conditions after a few weeks, developed into healthy plasmodia, such dormant bodies do not seem sufficiently dependable for maintaining the species in the laboratory.

It has been stated several times in this paper that *R. filosa* seemingly gives off minute spore-like bodies whose development has been difficult to follow. There also appears to be evidence in my cultures that slime molds may manifest a somewhat similar phenomenon. Such a phase in the Myxomycetes could, it seems, explain why some of them appear to lose vigor at certain times, either in whole or in part, and tend to die out if not given the care they need at this time. A full elucidation of this problem awaits further observation and experimental study.

*R. filosa* has been shown to have several characters in common with the Myxomycetes and Foraminifera. It is likely that more will be found. It seems possible that further studies may also reveal that this primitive organism, together with certain species of *Proteomyxa* which it resembles rather closely, may in time come to be regarded as members of a group that is more or less intermediate between the Myxomycetes and the Foraminifera.

#### SUMMARY

A hitherto unreported primitive plasmodium, *Reticulomyxa filosa*, has been discovered, which has among others the following characteristics and habits:

1. Aquatic and semiaquatic (fresh water), multiform, white plasmodium, without wall or other permanently formed membrane, remaining fairly stationary while vegetating, surrounded by an intricate network of anastomosing, filose pseudopodia arising from any point on the surface of plasmodium and extending to as much as ten times its diameter in search of food.

2. Protoplasm very active, finely and coarsely granular, undifferentiated into ecto- and endoplasm, multinucleate, vacuoles (noncontractile), not surviving slow desiccation.

3. Streaming in pseudopodia a simultaneous two-way or sleeve-type of flow; in central portion, which is often a thin broad sheet of protoplasm, many lines of flow alternately opposed and irreversible.

4. Plasmodium periodically clears itself of extraneous matter, moves to a new site, and undergoes longitudinal fission, usually resulting in three daughter plasmodia. Mature plasmodia seemingly disperse spore-like bodies when transferred to a fresh container of water, but the nature of reproduction other than by fission only vaguely understood at present.

5. Under water, plasmodial activities arrested both when subjected to lowered temperature and when cultured with certain algae.

6. Similarities to species of *Myxomycetes* and *Foraminifera* pointed out. Close affinity with certain species of *Proteomyxa* strongly suspected.

*Acknowledgments.* I wish to express my thanks and appreciation to those listed below, whose combined aid and encouragement have helped materially in making this report possible: Dr. John S. Karling, then of Columbia University; Dr. D. H. Wenrich, University of Pennsylvania; Dr. G. W. Martin, State University of Iowa; Dr. Joseph A. Cushman, Cushman Laboratory for Foraminiferal Research; Dr. William H. Weston, Harvard University; Dr. John Tyler Bonner, Princeton University; Dr. William D. Burbanck, Drury College; Dr. Asa A. Schaeffer, Temple University; Dr. Mary A. Pocock, R. U. C., Grahamstown, South Africa; Dr. Robert Chambers, Woods Hole; Dr. Libbie H. Hyman, American Museum of Natural History.

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## DETECTION AND OCCURRENCE OF ACID-PRODUCING FUNGI<sup>1</sup>

J. W. FOSTER AND HENRY DAVIS

For certain physiological problems and for surveys seeking organisms of potential industrial application it is desirable to examine large numbers of new strains of organic-acid-producing fungi. Three objectives may be satisfied by such a survey: (1) higher-yielding strains may be obtained with respect to any particular acid; (2) organisms may be obtained different from any known to produce a certain acid; (3) new acids may be found to be produced by fungi.

The following selective technique for isolation of acid-producing fungi has proved very satisfactory. It is based on color change of brom cresol green in the pH range between 5.4 and 3.8. Formation of organic acidity in a medium initially adjusted to pH 4-5 causes a marked change from blue-green or green to bright yellow. In agar plates the contrast is striking and the test very sensitive. Non-acid-formers cause no yellowing and simple inspection at once differentiates acid-forming fungi from non-acid-formers.

Since natural materials such as soil, manure, air, etc. are used as source materials, it is necessary to eliminate the bacteria and actinomycetes. This is accomplished by the original Waksman technique of adjusting the agar after sterilization to pH 4.0-4.5 with 1N HCl. The following points relate to the best working conditions. Medium: 5% glucose, 0.5% peptone, 0.1%  $\text{KH}_2\text{PO}_4$ , 0.05%  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ , 2% agar. The organic nitrogen source favors rapid growth and recovers maximum numbers of fungi. The high glucose concentration forces maximum acid formation by the fungi under these conditions.<sup>2</sup> The indicator is rather concentrated. One gram brom cresol green is ground in a mortar with 14.3 ml. 0.1 N NaOH. When solution is complete, it is diluted to 250 ml. with distilled water. The optimum concentration was found to be 6.7 ml. of this stock indicator solution per 100 ml. agar medium, added before autoclaving. This concentration had no detectable inhibition on the fungus population nor was it absorbed out of solution by the fungus mycelium like many of the other ordinary pH indicators tested. Pour plates of various dilutions of natural materials are prepared in the usual manner and incubated at 30° C.

Acid-producing colonies are detectable while they are still barely visible

<sup>1</sup>Supported in part by a grant from Ciba Pharmaceutical Laboratories, Inc., Summit, N. J.

<sup>2</sup>Foster, J. W. 1947. Some introspections on mold metabolism. *Bact. Rev.* 11: 167-88.

to the naked eye; for this reason early observation is desirable. This permits testing in relatively crowded plates where largest numbers of fungi are exposed for examination, the results being obtainable before overgrowth occurs. Use of 150 mm. petri dishes permits detection of acid-formers even though numerically they may be only a small proportion of the total fungus population. The matter of time-saving on incubation is an important feature.



Fig. 1. Yellow zones indicative of acid production by fungi. The background agar is deep blue-green, somewhat darker on the right side owing to uneven distribution of agar thickness. A, strong acid-producer with largest zone. B, moderate acid-producer. C, non-acid-producer.

Generally the picture of the young colony is charactersitic of the old one, though weak acid-formers may not be detectable as very young colonies. Nevertheless, the desired organisms, namely strong acid-producers, are unmistakably detected while colonies still one millimeter or less in diameter. The yellow acid zone surrounding the colony increases with the size of the colony; it is proportional in size and in intensity to the acid-forming ability of the organism (fig. 1).

The acid-formers are picked off before colonies grow together and inoculated on to petri plates of the same medium but adjusted to pH 6.5 at which value the indicator is its full deep blue; restriction of bacteria is unnecessary here. The acid-formation reaction in these plates is even more sensitive because the zones around larger colonies give a more reliable evaluation of the organisms than on the original crowded isolation plates.

Numerous checks in liquid media confirm the fact that the method selects acid-formers, though the relative degree of acid formation in liquid media is not necessarily the same as in the agar plates. However, any one liquid test medium used for a survey comparison will not, of course, be optimum for acid-production by all fungi.

Table 1 shows the proportion of the total fungus population which were clear-cut acid-formers as revealed by the above technique.

TABLE 1. *Acid-forming fungi in soils.*

Soil type	Optimum dilution	Average total count	Numbers of acid producers	Percentage of acid-producers
Manured garden	1/1000	25	4	16
Florist leaf mold	1/10000	18	2	11
Flower bed	1/1000	40	11	28
Flower bed	1/1000	17	1	6
Plowed field	1/1000	9	3	33
Plowed field	1/1000	15	2	13
Cotton field	1/1000	14	2	14
Wooded area	1/10000	14	1	7
Rut on roadside	1/1000	11	1	9
Bank of stream	1/10000	20	1	5
Corn field	1/1000	17	1	6

Average: 13.4

The most common acid-producer encountered was *Aspergillus niger*. Many other *Aspergilli* and *Penicillia* were in this group as were members of Mucorales and several unidentified fungi. Tentatively identified were *Aspergillus hidulans*, *A. terreus*, *Penicillium luteum*, *P. rugulosum*, *P. frequentens*, and the yeast-like *Pullularia pullulans*.

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THE TRICHOMES OF *PHYSARIA GEYERI*, *PHYSARIA*  
*AUSTRALIS* AND *LESQUERELLA SHERWOODII*:  
DEVELOPMENT AND MORPHOLOGY

SOPHIE JAKOWSKA<sup>1</sup>

Trichomes or epidermal hairs on the aerial parts of plants attracted the attention of early writers because of the peculiar structure and the characteristic silvery appearance they produced in pubescent plants. Thus the general morphology of trichomes was treated in the early descriptions of the plant epidermis from 1700 onward.

Since then, and particularly in the last century, various functions have been attributed to the trichomes. It is of interest to review some of these older opinions, although even today we do not possess sufficient evidence to establish any theory of the functions of trichomes. Poisson (1879) believed that hairs on plants such as *Phaseolus* were an adaptation to the environmental conditions. Arthur (1881) suggested that upon rapidly growing parts of plants, such as young flower buds, the abundance of delicate trichomes aids in supplying oxygen to the tissues. He believed this was analogous to oxygenation of some polyps and worms having external filamentous gills. Berthold (1882) on the other hand believed that trichomes protect the plant from excessive light. Tietze (1906) brought forward some evidence that trichomes were concerned with water intake in Bromeliaceae. Cannon (1908) referred to trichomes as a trichomal system. He believed that the trichomal system offers a favorable field in which to study the origin, development and biological relationships of plant organs, inasmuch as it is comparatively little affected by other tissue systems. He pointed to the fact that in some species trichomes take on the function of photosynthesis, thus becoming entirely independent for their nutrition. Harvey (1919) performed experiments from which he concluded that undercooling of the tissues occurs to a greater degree in herbaceous plants with trichomes. Sayre (1920) believed that trichomes are related to transpiration of the leaves.

Most of the older workers who considered trichomes as a means for classification have availed themselves of both herbarium specimens, including sections prepared from such dried specimens, and fresh living material. More recently Molby (1931), who studied trichomes in Malvaceae, boiled

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fresh leaves for a few minutes in water, then removed the trichomes under the binocular. The trichomes were placed in a small drop of water on a slide and allowed to dry, then mounted in Canada balsam. Wright (1945) studying the epidermal characters in *Fraxinus* followed a method which consists in obtaining collodion peels made by applying a solution of collodion in butyl acetate plus 5 per cent butyl alcohol to the under surface of the leaf.

In the present study living and herbarium specimens have been used, but greatest emphasis has been placed on the cytological preparations consisting of leaf sections and smears, which permitted observation of changes within the nucleus at various stages of trichome development.

Most previous investigators were concerned for taxonomical reasons with the morphology of fully differentiated trichomes, rather than with their origin and development. Very few were concerned with the nuclear phenomena.

Arthur (1881) described incipient trichomes on the surface of anthers, which arose through an enlargement of some epidermal cells protruding to the outside. Tietze (1906) described the development of a multicellular stellate trichome in Bromeliaceae, which arises from epidermal cells. Cannon (1908) attempted to determine the sequence of the cell wall formation in a multicellular trichome in walnuts and sketched 6- and 8-celled trichomes showing the cell lineage of each. Rosenvinge (1911) studied hyaline unicellular simple hairs in a family of marine algae. He noticed that they arose through the metamorphosis of superficial cells and were not cut off from the apical cells as special hair cells. In the fully grown trichomes he observed only a thin layer of protoplasm and limpid cell sap within the cell, but during the process of development he observed changes in the position and in the shape of the nucleus, which according to him becomes transformed into a crystalloid in the latest stage and then stains deep blue with hematoxylin. He also noticed that these hairs often decay long before the cessation of growth. Brockmann-Jerosch (1914) affirmed that in the grasses he studied trichomes arise on the young leaf blade from a young cuboidal epidermal cell through a protrusion of the outer wall. He described the changes in the walls of the trichomes without considering the nuclei. In some of the grasses described by him the unicellular simple trichomes attain extremely large size.

A fairly recent paper in which the development of the trichomes was described in detail and from a cytological viewpoint was that of Cooper (1932) on *Shepherdia canadensis*. This author followed the stages of development of a multicellular peltate trichome, giving great attention to the relative position of the nuclei and the orientation of the spindles during divisions. He traced the cell lineage and determined the origin of the cells of the stalk and of the shield in the formed peltate trichome.

Trichomes in *Physaria Geyeri*, *P. australis*, and *Lesquerella Sherwoodii* are unicellular stellate structures. Beginning as epidermal cells the trichomes in these species reach an unusual size and exhibit during the whole process of growth and differentiation nuclear changes of considerable cytological interest.

The characteristics of the trichomes permit differentiation between the three species under investigation. For the same reason Vanatta (1907) and Payson (1921) attached great importance to the trichome size and shape as a means of differentiating species within the genus *Lesquerella*. Although it has been impossible in the present study to establish one single trichome type for each of the three species, there is no doubt that the general characteristics of the pubescence may play an important part in the taxonomical determinations.

Rollins (1939) states that *Physaria* and *Lesquerella* are not easily recognized as distinct genera if only flowering plants are considered, though their fruits differ. But even in these respects certain species of *Lesquerella*, namely *L. Kingii* and its close relatives, approach the condition found in such species of *Physaria* as *P. Geyeri*. This relationship was pointed out by Payson (1921). As Rollins states on the basis of his cytological studies of meiotic chromosomes, the cytological evidence also indicates a closer relationship between the two genera than that attributed to them by some taxonomists, although there is no question as to the separation of these two genera.

With these facts in mind it has been attempted in the present study to bring in a few similarities and differences in trichome form and development in the representatives of the two genera in question. The main purpose of this investigation was, however, to follow the nuclear phenomena in the unicellular stellate trichomes of *P. Geyeri*, *P. australis* and *L. Sherwoodii* through the process of growth and differentiation.

**Material and Methods.** Living and herbarium specimens of *P. Geyeri*, *P. australis* and *L. Sherwoodii* were made available through the courtesy of Dr. Bassett Maguire, Curator of the New York Botanical Garden, who collected and identified the plants. The living specimens were raised to maturity from seeds in the greenhouses of the New York Botanical Garden.

The places of origin of the plants were as follows: *P. Geyeri*, 26715, Nine Mile Falls along the Spokane River, Washington, July 22, 1946; *P. australis*, 25408, O'Donall Canyon, West Slopes, Paradise Range, Nevada, June 12, 1945; *L. Sherwoodii*, 27057, above Slick Rock Creek in vicinity of Hurricane Creek, Wallowa Mountains, Oregon, August 16, 1946. The parent plants from which the seeds were derived were available also as herbarium specimens, except for *P. australis*.

The cytological studies on trichomes were done by means of Feulgen smears after 3:1 alcohol-acetic fixation. Light green counterstain was used to show the cytoplasm to a greater advantage. Smears were made of various portions of the 6-week-old plants and of the leaves from the older plants. Sections of the young plants were made and stained with iodine and gentian violet.

The observations, measurements, and counts were carried out under 15x ocular and 98x objective for cytological material and with a 15x ocular and 10x objective for the herbarium and living material.

**Observations and Results.** In the course of the investigation it became necessary to compare the general morphology of the trichomes fixed in acetic alcohol, and stained by the Feulgen reaction, with the living and dried specimens. Trichomes have not been studied previously by the smear method and it was necessary to determine to what extent the trichome shape was altered in the smear preparations. At the same time a more careful study of living and herbarium specimens has been encouraged by the evident need of more information on the morphological features of the two genera *Physaria* and *Lesquerella* and the fact that some authors greatly relied on the trichome shape and size for the differentiation of the species within these genera. Since the comparison between the smeared, living, and the herbarium material seemed to indicate that it is possible to obtain good cytological preparations without significant alteration of the shape of the trichomes, it has been judged proper to describe the various stages of trichome development as they appeared in the Feulgen-stained smear preparations.

*Cytological Observations on the Development of the Trichomes.* In the 6-week-old plants, most of which were less than 1 inch above the soil and still bearing the cotyledons, it was already possible to observe all stages of development of the epidermal hairs on the stem and leaves. *Physaria Geyeri* is the species for which the whole process is described in detail. In the two other species of plants under investigation the process was essentially the same. The trichomes of *P. Geyeri*, however, were the simplest of the three and this facilitated the description.

The trichomes originate from the epidermal layer of the actively growing regions of young leaves and stem. They do not occur on cotyledons, as was already pointed out by Rollins (1939) for plants of the same genera. The trichomes do not develop synchronously, for the various stages of development can be found together. An actively growing region of the leaf bud in a 6-week-old plant is reproduced in figure 1. It can be seen that some of the epidermal cells elongate in the direction of the free leaf surface. The main portion of the cell remains in its position among the epidermal cells and

forms the stalk of the future structure. The nucleus at the early stage is located within the portion of the cell adjacent to the epidermal cells. Later, the cell elongates and sends out projecting arms parallel to the leaf surface.

In the section seen in figure 1 only two of the developing parallel branches or arms can be observed. These continue to grow parallel to the surface of the epidermis and apparently remain straight, giving the effect of a star-shaped shield. Even at the stage seen in figure 1 the section of the trichomes shows only a bulb-like enlargement, partially expanded. The structure of the developing shield is rosette-like, when viewed from the top,

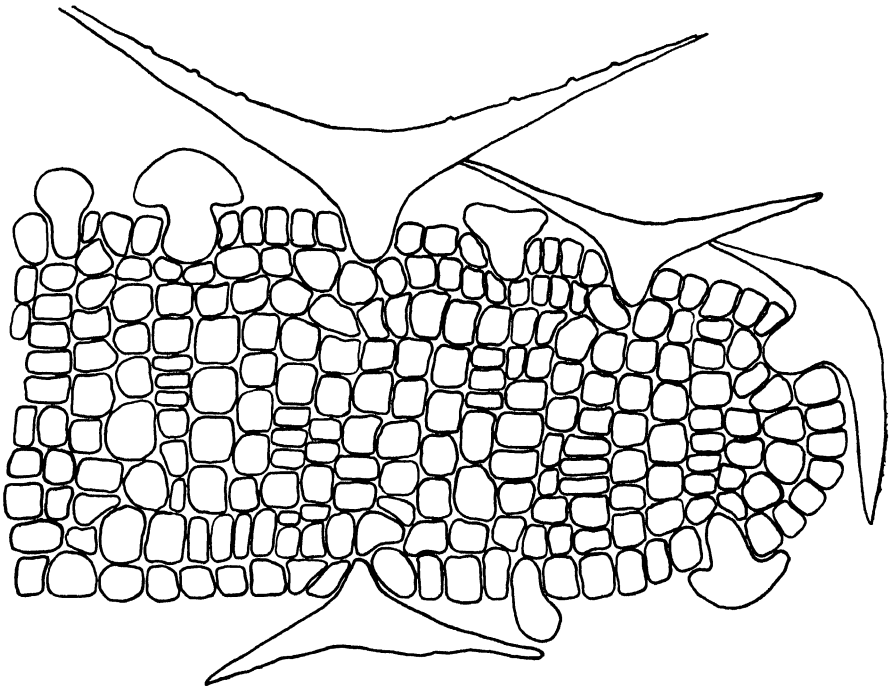
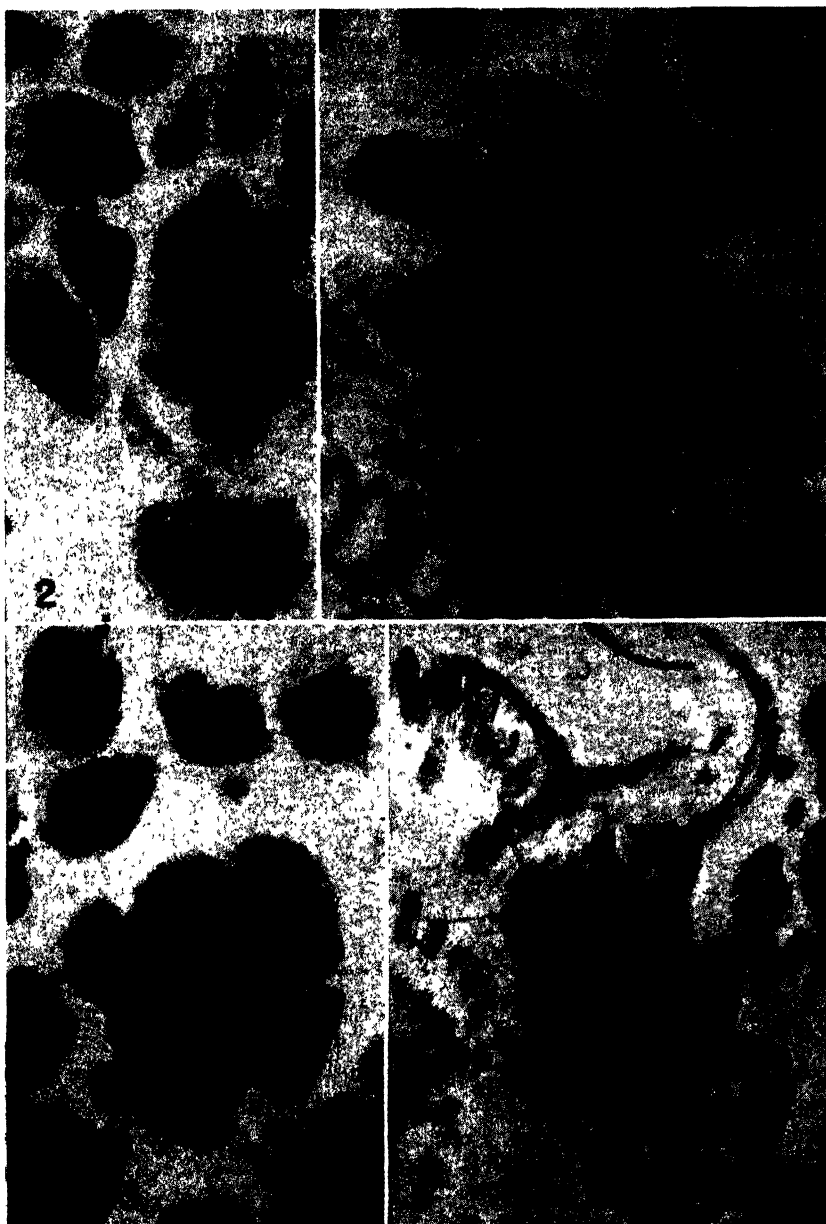


FIG. 1. Longitudinal section through a leaf of a six-week-old *Physaria Geyeri*. Camera lucida drawing.  $\times 750$ .

as is easily seen in the smear preparations. At the stage when the trichome is fully developed the outer cell wall becomes thickened, forming knob-like projections. There is no considerable change in position of the trichome cell throughout the entire process. The stalk portion of the cell becomes either slightly depressed below the level of the epidermal cells or retracted to a certain extent. The nucleus, as long as it remains normal in appearance, occupies the central position in the stalk region, but at the level of the developing trichome branches. No septa are formed within this large unicellular structure. The relative increase in size of the trichome cell from the



FIGS. 2-5. Leaf smears from adult specimens of *Physaria Geyeri* stained by Feulgen reaction and light green. All  $\times 1960$ . FIG. 2. Epidermal cells showing heterochromatic bodies. FIG. 3. Expanding epidermal cell. FIG. 4. Cell showing development of trichome branches. FIG. 5. Condition of the nucleus of a developing trichome at a later stage: enlarged heterochromatic bodies and nucleolus.

initial to the final stages of the development, and the cytological phenomena involved, are best followed in the smear preparations which allow a surface view of the trichome's branching portion.

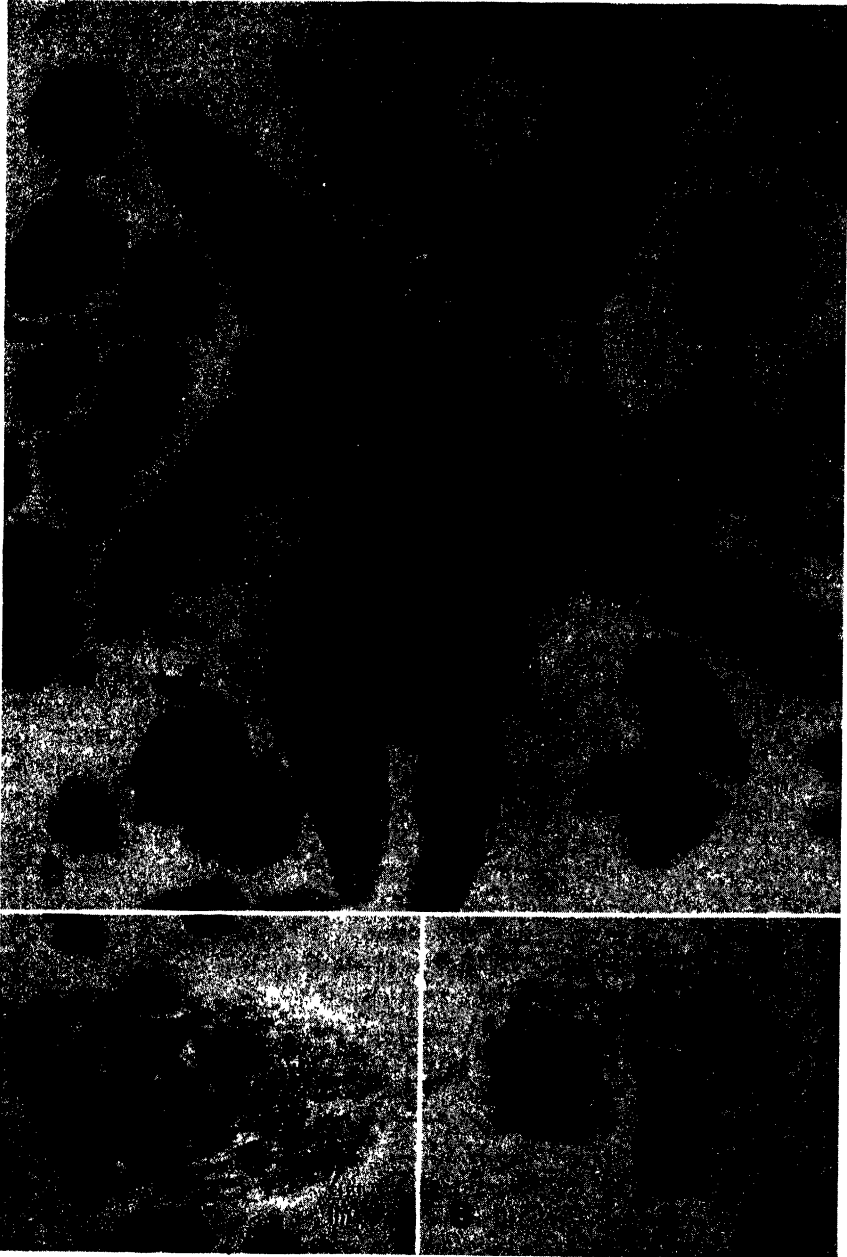
The consecutive stages in the development of a trichome of *P. Geyeri* as observed in Feulgen-stained leaf smears are shown in figure 2-6. It can be seen in figure 2 that the nuclei of the epidermal cells are in a characteristic prochromosome stage. The nucleus is filled with large and small globules of heterochromatin, not obviously related in size or number to the chromosomes. Among the epidermal cells some can be distinguished as having a greater amount of cytoplasm. In such cells at a later stage (fig. 3) the cytoplasm is seen protruding in an amoeboid fashion. A similar type of epidermal cell in *P. australis* shows a slightly different appearance of heterochromatin. There definite chromatin bodies are observed but a large amount of chromatin material is seen dispersed throughout the nucleus. Some of the epidermal cells, although not having an enlarged nucleus, show a characteristically larger amount of cytoplasm, and consequently a greater cell surface. Such a stage, seen in figure 2, corresponds to the bulb-like stages seen in figure 1.

From this stage on, the cell wall has pseudopodium-like processes and the nucleus enlarges (fig. 4). The nucleus contains about the same number of heterochromatic bodies but they are greatly enlarged. The response of these bodies to the Feulgen reaction is as deep as that of the heterochromatic bodies in the epidermal cells, but occasionally vacuoles can be seen in the largest ones. In the photomicrographs that follow, it is possible to observe an enormous increase in the amount of cytoplasm and of chromatin. The nucleolus also enlarges during this process. This can be seen by comparing the nucleolus which appears as a grey body in one of the small epidermal cells (fig. 8) with that, in a developing trichome (fig. 7) at a stage similar to that in figure 6.

The further increase in size of the entire trichome cell cannot be illustrated at the same magnification. An epidermal cell with an original length of about  $10\ \mu$  becomes a unicellular structure  $450\text{--}750\ \mu$  in diameter.

In most trichomes when a certain size is reached the increase in amount of chromatin within the nucleus stops. The heterochromatic bodies become vacuolated and do not stain so deeply with the Feulgen reaction as they did at earlier stages. Further changes in the nucleus then take place. It is often possible to see in sectioned material a fully developed trichome containing somewhere in the stalk region the remains of the nucleus in form of a lobed body which no longer responds to the Feulgen reaction.

It is almost impossible to determine at what stage of trichome development the deterioration of the nucleus takes place, but it is evident by the time the characteristic thickenings appear on the cell wall. The fully formed



FIGS. 6-8. Leaf smears from adult specimens of *Physaria Geyeri* stained by Feulgen reaction and light green. All  $\times 1960$ . FIG. 6. Full view of developing trichome. FIG. 7. Nucleus of a developing trichome showing enlarged heterochromatic bodies and nucleolus. FIG. 8. Epidermal cell showing small nucleolus and heterochromatic bodies.

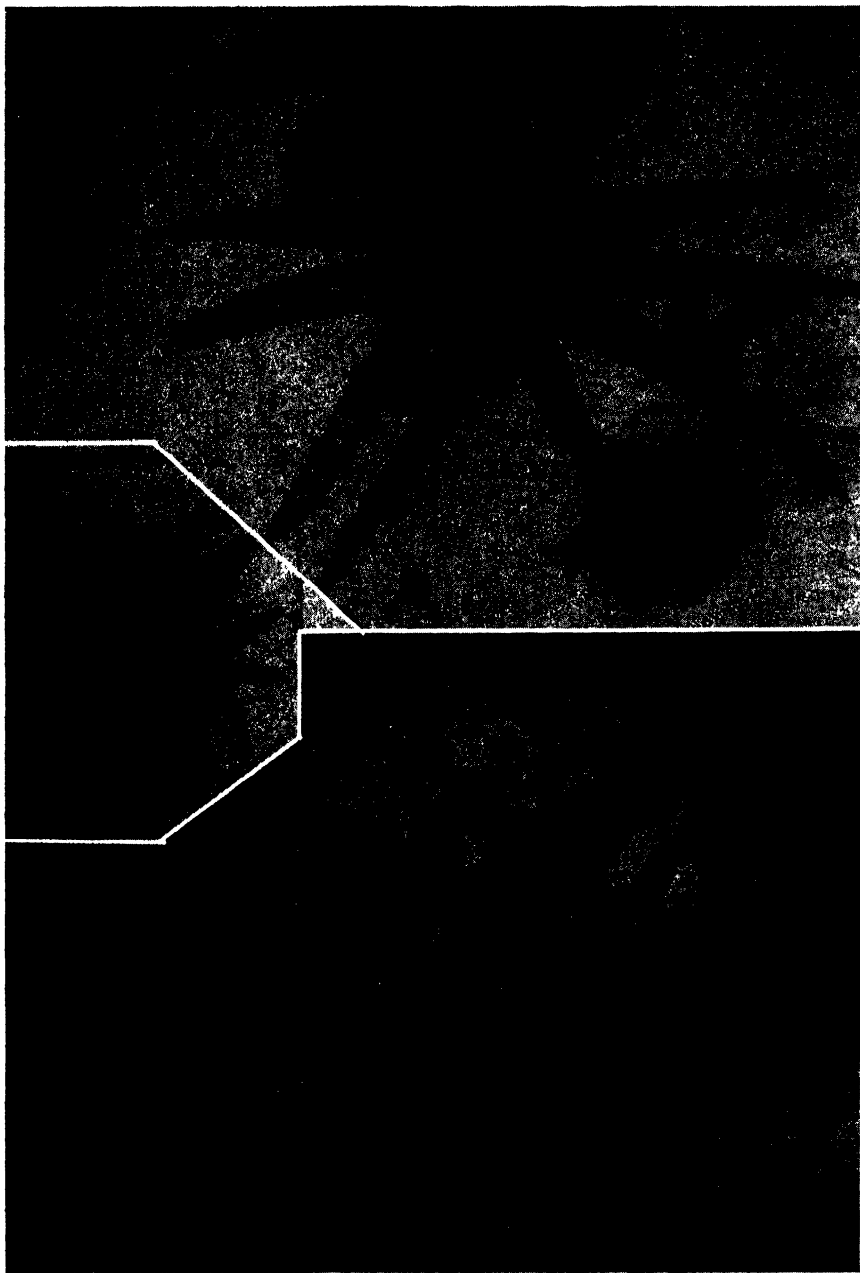
trichome is a structure consisting of cell wall, the surface of which is covered with elevations such as are visible on a trichome in figure 1. The full view of the trichome branches in *P. Geyeri* after complete differentiation can be seen in a smear (fig. 9). This is the final stage in the growth and the development of the trichome. Similar stages for *P. australis* and *L. Sherwoodii* can be seen in figures 10 and 11.

*Morphology of Adult Trichomes.* This study was initially undertaken in order to compare the general appearance of fully differentiated trichomes in stained smear preparations, herbarium specimens, and living plants. It was necessary to find out whether or not the process of fixation and the hydrolysis preceding the Feulgen reaction altered considerably the shape of the trichomes.

For the study of the living material the following were available in the greenhouse: 4 specimens of *P. Geyeri*, 1 specimen of *P. australis*, and 4 specimens of *L. Sherwoodii*. A few older and younger leaves and flower shoots were taken from each plant and examined immediately under magnification of 125 $\times$ . It has been noticed that only fully developed trichomes could be studied by this method, since the earlier stages were obliterated beneath the dense covering of trichome branches. In *P. Geyeri*, leaves of greenish and silvery color were observed, but regardless of color the upper surface of the leaves was covered with dense trichomes, apparently uniform in size. The lower surface of the leaves was covered with fully differentiated trichomes much smaller in size. The elongated basal portion of the leaf blade was the area most densely covered with trichomes. The branches of the trichomes in a living plant were uniformly straight and were not bent or twisted. The thickenings on the wall of the trichome branches were clearly visible. The trichomes were spaced so as to permit counting the branches on the individual trichomes. From 50 counts taken from the leaves with a silvery coloring the number of trichome branches varied from 9 to 17, while from 50 counts from leaves with a greenish coloring the number of branches per trichome varied from 7 to 12.

The trichomes appeared to be nearly uniform in circumference. The pattern in trichome branching was not uniform. Observation of the upper surface of the leaf with the trichomes undisturbed in their natural position revealed nine basic recurring patterns in the branching of trichomes. Few trichomes were symmetrical. Radiating branches on the individual trichomes were not of uniform length. Frequently one branch was exceptionally long. Such long branches did not always arise from the central region but commonly were derived from dichotomous branching. The various patterns are represented by diagrammatic drawings (fig. 12) in which the relative length and position of the trichome branches are shown. The lines represent a





FIGS. 9-11. Fully developed trichomes as seen in leaf smears stained by Feulgen reaction and light green. All  $\times 200$ . FIG. 9. Trichome of *Physaria Geyeri*. FIG. 10. Trichome of *Lesquerella Sherwoodii*. FIG. 11. Trichome of *Physaria australis*.

hypothetical midline for each trichome branch starting at the center of the basal region of the branch and ending at the distal end. It can be noticed that dichotomous branching occurs in many branches. Pattern *A* was rather unusual and not so frequently found as the others. In this pattern dichotomous branching does not arise until after a certain development from the base of the original four radiating branches. Pattern *B* shows a similar arrangement except that one original branch never divides dichotomously. Pattern *C*, *D*, and *G* show one disproportionally long arm. In pattern *D* there is almost no clear-cut dichotomous branching. A secondary dichotomous branching can be seen in pattern *H*.

Four specimens of *L. Sherwoodii* were available and several leaves were taken from each plant. The color of the leaves varied from silvery green to green as in *P. Geyeri*. The trichomes, however, appeared smaller in *L. Sherwoodii* than in *P. Geyeri*, but were more compact and more nearly peltate, with the central region larger than in *P. Geyeri*. The branches of the individual trichomes were not located in the same plane. This made counts and pattern-determination difficult. The number of branches encountered on individual trichomes was 13, 14, and 15. The counts did not essentially differ on the upper and the lower surfaces of the leaf. In *L. Sherwoodii* most radiating branches divide dichotomously and there are few single branches arising from the central region. There has been some difficulty in establishing the most frequent patterns in *L. Sherwoodii*, but the following two were most commonly encountered. Pattern *J* showed the arrangement in a 14-branched trichome. Four main branches divide dichotomously at some distance from the center while 3 other main branches evidently divide at the very center. In pattern *K* also of 14 branches, each of the 7 main branches divides at some distance from the center, but the whole trichome is not perfectly radially symmetrical.

The observed leaves of *P. australis* were all from the same plant, silvery green in color. The trichomes appeared larger than those of *P. Geyeri* and *L. Sherwoodii*. The dense pubescence made the counts of trichome branches difficult. The number of branches on individual trichomes was seldom lower than 20. The branches of each trichome extended in more than one plane. In stained preparations the shape of such trichomes was altered by pressing all the branches into one surface. The branches were more uniform in length than in the two other species. Thus the outline of the trichome appeared circular. In this species, as in *L. Sherwoodii*, it was difficult to determine trichome patterns. A pattern with 27 branches was seen quite frequently. In this type of trichome, as shown in pattern *L*, there are seven main branches with a primary and secondary dichotomous branching. The failure of one branch to divide results in the total of 27 instead of 28 branches.

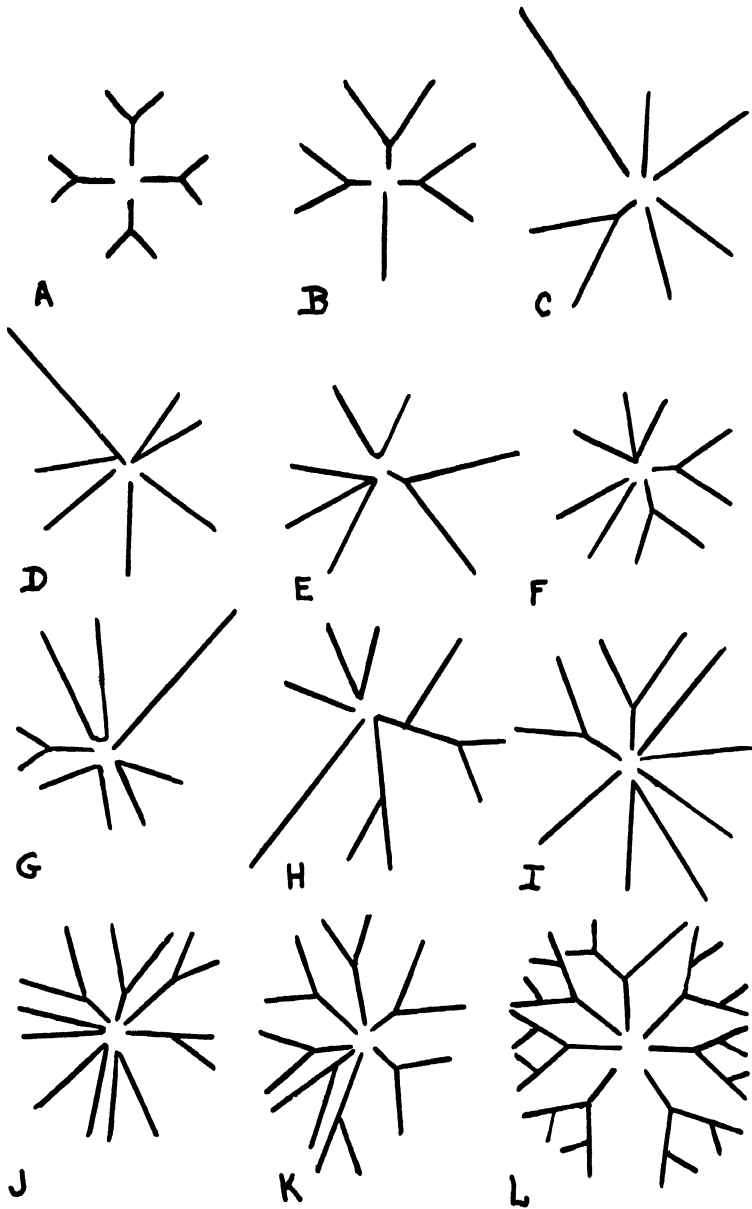


FIG. 12

FIG. 12. Diagrammatic representation of trichome patterns from living material. A-I, *Physaria Geyeri*. J-K, *Lesquerella Sherwoodii*. L, *Physaria australis*.

Nine specimens of *P. Geyeri* Gray and ten specimens of *L. Sherwoodii* Peck from the herbarium of the New York Botanical Garden were studied under a 9x ocular and a 4.8x objective.

It was observed that dried trichomes were essentially identical in shape with those of the living plants. In *L. Sherwoodii* trichomes were very dense on the upper portion of the leaf and on the leaf blade, but less dense on the flower-bearing shoots. The trichomes were translucent. The number of branches observed on individual trichomes varied between 8 (10) and 17. Similar observations on the distribution of trichomes were made in *P. Geyeri*. The number of branches on individual trichomes varied between 8 and 12. It appeared from the observation on these few herbarium specimens that the size of trichomes varies from plant to plant, probably with the age, and on the plants with larger trichomes the number of branches on individual trichomes appeared to be higher. The counting of branches on the individual trichomes was difficult because of their proximity.

The stained preparations provided material for a more detailed study of fully developed trichomes. As was shown in figure 1, fully developed trichomes can be already found on the young leaves of 6-weeks-old plants. They were previously described as the final stage in development and differentiation. The fully developed trichomes of the three species can be compared in figures 9, 10, and 11. These trichomes were chosen at random from the stained smeared preparations and are shown with the same magnification. Thus only the surface view of the radiating branches can be seen. The trichome of *P. Geyeri* shows thickenings on the wall characteristic of the fully differentiated trichome. The branches all lie in the same plane. The trichome of *L. Sherwoodii* exhibits the same thickenings on a relatively higher number of branches. The diameter of the entire trichome appears however much smaller. Apparently the several branches which in the natural condition lie in different planes have been compressed into one plane by the smear technique, giving the trichome an artificially enlarged central region which imitates the shield of a peltate trichome. The trichome of *P. australis* is not shown in perfect focus. This was done in order to emphasize the difference between this giant differentiated cell and the epidermal cells, one of which gave rise to it. The surface of the branches is covered by the same kind of thickenings. In the center the opening caused by tearing off the trichome stalk can be observed. The trichome appears to be the same size as that of *P. Geyeri* but it has a much larger number of branches. These branches are not like those of *P. Geyeri* and are apparently compressed into one plane by the smear method.

It has been a question whether or not to consider these photographs as representative of the trichomes of the three species under study. It has been revealed by previous study of the living and herbarium material that there

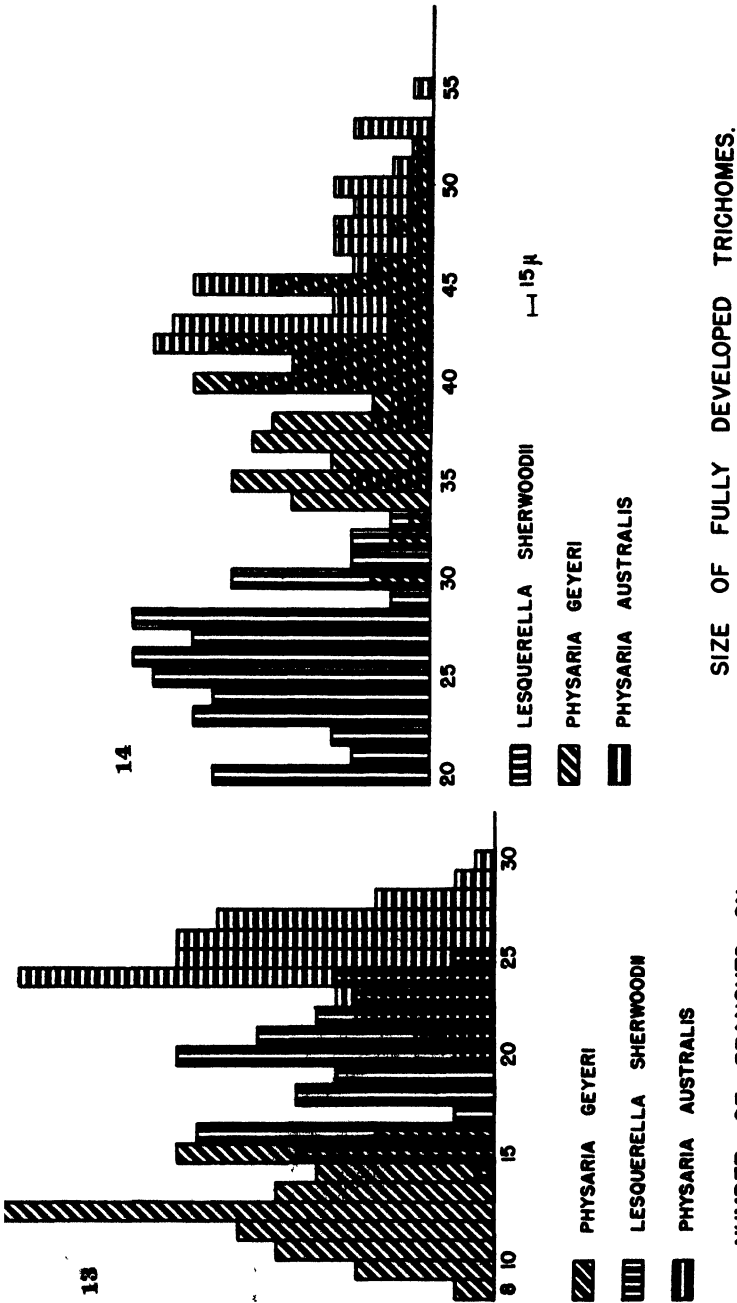


Fig. 13. Histogram representing the distribution of the number of branches on fully developed trichomes of *Physaria Geyeri*, *Physaria Australis* and *Lesquerella Sherwoodii*. Fig. 14. Histogram representing the variation in size of fully developed trichomes of *Physaria Geyeri*, *Physaria Australis* and *Lesquerella Sherwoodii*.

seems to be great variability in size of the trichomes and in the number of branches on the individual trichomes within the species. For this reason it was proposed to investigate further, although again on a limited number of plants, the sizes and the number of branches of the trichomes.

From previous studies on living and herbarium specimens it was observed that there was no number of trichome branches characteristic for each species. One hundred trichomes from 10 different slides taken from various specimens were examined for each of the three species. No general conclusions are attempted. It is possible, however, to state that in the three samples the numbers of branches of the individual trichomes are distributed within three different ranges. In 100 trichomes of *P. Geyeri* which were examined, the number of branches varied from 8 to 16. Twenty-five trichomes out of this sample of 100 had 12 branches. In *L. Sherwoodii* the number of branches varied from 14 to 25 and in *P. australis* from 20 to 30. These results are seen in figure 13.

While examining slides of Feulgen-stained material one easily forms the impression that it is possible to distinguish between the material from the three species by trichomes alone. It seems that in general the trichomes of *P. Geyeri* have fewer branches, those of *P. australis* have more numerous branches, and those of *L. Sherwoodii*, although with numerous branches, can be distinguished by the condition of the prochromosomes in the neighboring epidermal cells and by the trichome size. The different appearance of the prochromosomes will be described elsewhere. The size of the trichomes in the three species has been studied from the stained specimens. The measurements were taken by choosing the maximum trichome diameter from tip to tip of the opposite branches. From the plotted results (fig. 14) it appears that the values for *L. Sherwoodii* are much lower than for either *P. Geyeri* or *P. australis*. Thus the general impression that the trichomes in the available specimens of *L. Sherwoodii* are smaller seems to be corroborated by these data, although this statement cannot be validly made about the trichomes of *L. Sherwoodii* in general.

**Discussion.** There seems to be no disagreement, among the authors who described the development of trichomes, as to the cells from which the trichomes originate. The process by which unicellular stellate trichomes described in the present paper grow and differentiate is more striking, however, than most cases in which a more complex multicellular epidermal hair forms by repeated cell divisions. The trichomes of *Physaria* and *Lesquerella* here described arise from epidermal cells which apparently in the initial stages do not differ from the other epidermal cells. The first sign of their differentiation is the increase in the amount of cytoplasm and most of the growth takes place when the cell nucleus and cytoplasm appear normal.

Whatever the forces are that influence some of the epidermal cells to increase their volume and surface to such great extent and to undergo such profound changes in the cell shape they do act selectively on certain cells. In the sections of *Lesquerella* and *Physaria*, trichomes have never been found arising from adjacent epidermal cells, although the plants have an abundant pubescence.

In the process of differentiation of the stellate trichomes it was observed that the cell fails to undergo mitosis, although the cell surface increases rapidly. Even more spectacular is the increase in the amount of chromatin within the nucleus of the trichomes. The resting condition of the nucleus in *Lesquerella* and *Physaria* is characterized by massive heterochromatic bodies. The chromatin in *P. Geyeri* and in *L. Sherwoodii* is condensed in more definite bodies than that of *P. australis*, the nucleus of which contains large amounts of chromatin distributed throughout in form of minute granules. Studies on the heterochromatin are in progress. The increase in amount of chromatin during the development of trichomes can be judged from the increased size of the nucleus and of the individual prochromosomes. The heterochromatic bodies in the very young trichomes respond as intensely to the Feulgen reaction as do the large ones in a nearly differentiated trichome. There is apparently not sufficient vacuolation of the heterochromatic bodies to account for such enormous increase in size. There seems to be no "dilution" of chromatin within an enlarged prochromosome-like matrix. It seems that the size increase in the nucleus of a developing trichome is verifiable. The nucleus remains in the resting stage while the cell growth takes place. This suggests that within this resting nucleus chromatin reduplication takes place. It is difficult to judge whether or not at the final stage the cell reached a high degree of polyploidy. If the size of the nucleolus were a reliable feature by which to determine polyploidy, the view that trichomes become polyploid during their development could be supported by actual evidence (figs. 7, 8). As was previously stated, the nucleus of a differentiating trichome remains in the resting condition. It maintains its position near the center of the stellate structure, slightly below the upper surface of the stalk region, while undergoing an increase in size. At the same time the cell attains an enormous size by extrusion of pseudopodium-like processes, which are referred to as trichome branches in the present paper. In the initial stages of development the cytoplasm fills the entire cell and its branches. The vacuole is relatively small. As the branches of the trichome elongate and become more numerous, a larger vacuole appears and the cytoplasm coats only the inner portions of the trichome walls in a thin layer. The cytoplasm thus increases in amount up to a definite limit. This probably occurs before the cell wall and the nucleus complete their growth.

During the process of branch formation the trichome can be considered

an elongating cell so long as the nucleus, which increases in size, retains a normal appearance. Until such a state is realized, it might be possible to arrest the process by preventing differentiation, which is accompanied by disintegration of the nucleus and the thickening of the cell wall. Before the irreversible nuclear changes take place, it might be possible to stimulate nuclear division in the fairly large trichome as was possible for elongated cells of *Allium cepa* by chemical treatment (Berger 1946). In such a case the suspected polyploidy of the trichome might be revealed even if the actual cell division failed.

One might be inclined to believe on the basis of the observations made that in trichomes of the three species the actual growth can be influenced independently of the process of differentiation. In the herbarium specimens consisting of adult plants, fully differentiated trichomes of much smaller size could be occasionally seen among the larger ones, but most of these were limited to certain regions such as the basal elongated portion of the leaf blade and the lower surface of the leaf. Wherever such small trichomes were found in the smear preparations, it could be noticed that the pseudopodium-like branches arose in cells with a smaller amount of cytoplasm. The nucleus in such cells has not the ratio to the cytoplasm that exists in larger trichomes. Thus it seems that in cells giving rise to smaller trichomes, the differentiation is speeded up, taking place at an earlier stage, and the period of growth is shortened. If one considers that at the time the trichome becomes differentiated and its nucleus deteriorates the sister epidermal cells have nuclei which are able to undergo mitosis, one is impressed by the fact that cells of apparently the same origin are endowed with different growth habits and life spans.

Rosenvinge (1911) noticed that in the marine algae the trichomes deteriorate long before the plants die in autumn. This probably occurred because dead structures consisting of cell wall, non-functional nucleus, and dead cytoplasm could not resist the influence of salt water in which they were immersed. In land plants in a rather arid habitat the trichomes are well preserved long after the cell division in the leaves have stopped. Still the life span of a trichome is undoubtedly shorter than that of the epidermal cells.

It is difficult in the present study to draw any quantitative conclusions on the increase in volume of the cell relative to the increase in volume of the nucleus. If one considers in *P. Geyeri* the diameter of smallest epidermal cell nucleolus as 4 units in respect to 10 units of nucleolar diameter in a trichome at a late stage, as seen in figures 8 and 7, the increase in volume could be expressed as a ratio 8 : 125 or as 1 : 16. The diameters of the nuclei in the same cells would be relatively equal to 10 and 30 units, and thus the relative nuclear volumes would be in the ratio of 1000 : 27000 or 1 : 27. If



the cell volumes are considered, there are even greater difficulties than those connected with the arbitrary choice of cells the nuclei and nucleoli of which must be considered roughly as spheres. The main difficulty in the arbitrary choice of adult trichome is the observed variability in number of branches.

From a study of a few available living and herbarium specimens, including the Feulgen smear preparations, it is hardly possible to make any generalizations on the relationships between the three species on the basis of trichome size, form, and other features. This would require a survey of a large number of plants. It appears however that the plants of each species showed uniform variability in trichome size and number of branches on individual trichomes. It also appears from the bimodal distribution that dichotomous branching plays an important role in the determination of the number of branches on individual trichomes. The various patterns observed on the same leaf seem to make the task of differentiation of species by trichome shape an impossible one. These patterns were reported as most numerous for *P. Geyeri*. It is possible that an equally large number of patterns can be found in *L. Sherwoodii* and in *P. australis* but it is more difficult to determine this because of the large number of branches on individual trichomes. The distribution zones in the number of branches on individual trichomes and in trichome sizes suggest that these two features of the trichomes might be of some help in the taxonomical studies of these two genera of cruciferous plants.

#### SUMMARY

1. Unicellular stellate trichomes in *Physaria Geyeri*, *Physaria australis*, and *Lesquerella Sherwoodii* have been studied in Feulgen-stained smear preparations and in sections, as well as in living and herbarium material.

2. The process of trichome development has been followed in the three species and described in detail for *Physaria Geyeri*. In the latter during the process of trichome differentiation from epidermal cells, the volume of the entire cell as well as of the nucleus, nucleolus, and individual heterochromatic bodies increases considerably. As a result of this process an epidermal cell about  $10\ \mu$  in length becomes a stellate unicellular structure  $450\text{--}750\ \mu$  in diameter. The average final nuclear volume in *P. Geyeri* is 27 times that of the initial nuclear volume and that of the nucleolus approximately 16 times the initial nucleolar volume. It is difficult however to judge whether or not at the final stage the cell reaches a high degree of polyploidy, although the amount of chromatin within the nucleus increases while the nucleus remains in a resting condition.

3. Fully grown trichomes consist of numerous branches varying in number from 8 to 16 in *P. Geyeri*, from 14 to 25 in *L. Sherwoodii*, and from 20

to 30 for *P. australis*. The adult trichomes of *Lesquerella* are smaller than those of either *P. Geyeri* or *P. australis*. Several patterns of trichome branching have been observed for each species.

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## THE GENUS ALFAROA

WAYNE E. MANNING<sup>1</sup>

*Alfaroa*, described from Costa Rica by Standley (1927a), is one of the most interesting genera in the Juglandaceae.

Intensive studies by the writer on the inflorescences, pistillate flowers, and staminate flowers (Manning 1938a, 1938b, 1940, 1948) of all members of the family including *Alfaroa* have shown that part of the description by Standley was inaccurate and incomplete. Furthermore, recent collections made for the writer by Dr. Alexander Skutch have furnished a more complete knowledge of the staminate inflorescences and the internal structure of the fruit. This genus is one of the most primitive members of the family, as shown by studies by the writer and by Heimseh and Wetmore (1939). For these reasons it seems necessary to give a corrected description of its flowers, fruit, and other features, with a discussion of its relationships.

A few paragraphs from the letters of Dr. Skutch are of significance:

"... Upon receiving your renewed inquiry about *Alfaroa*, I found a single sterile specimen here in the museum, identified by Standley. Then I recalled that at Vara Blanca I had seen a small tree of that appearance. In June or July it bore unripe fruits. . . ." Recalling these facts, I thought it worth while to return to my old collecting ground for another look. Passing through the woods, I had the good luck to stumble upon a flowering tree which had just been felled for lumber and was still fresh. The foliage of this lofty tree was so different from that of the specimen of *Alfaroa* I had examined that at first I thought it must belong to a distinct species, possibly an undescribed species of the Juglandaceae. Certainly but for the chance of running into this fallen tree, I would not have collected material from the lofty and difficult trees of this appearance as *Alfaroa costaricensis*. But later, examining other individuals, I connected this one with the specimen in the museum, which evidently came from a young tree or a stump sprout. Stump sprouts bear young shoots and foliage with prominent long pubescence; the leaves of mature trees are nearly glabrous. The numerous leaflets on the leaves of stump sprouts are acute and conspicuously dentate; old trees have fewer leaflets to the leaf and these are blunt at the apex and sparingly if at all dentate. The herbarium specimens I have for you show these differences quite clearly. They also show that the leaves are sometimes borne three at a node.

"As I was returning from what I considered a successful trip, I found a large fallen branch of *Alfaroa* lying beside the road. It bore numerous long staminate catkins in liberal clusters; there was no pistillate inflorescence among them. This heavy branch broke from a great tree at least one hundred feet high and about three feet in diameter at breast height, where the trunk was deeply furrowed and ridged. Examining the lofty crown through my binoculars, I could see no pistillate inflorescences; but because of the great height of the tree this negative evidence is possibly not conclusive.

<sup>1</sup> The writer wishes to express appreciation to the curators of the herbarium at the Chicago Museum of Natural History and of the U. S. National Herbarium for their generosity in lending specimens. The drawings were made by Grace A. Petersen and Donald C. Baird, Jr.

I think it probable, however, that *Alfaroa* is polygamo-dioecious. The predominantly pistillate trees bear small staminate aments at the bases of some of the pistillate spikes, as stated in the original description of the genus; but there are also trees (or at least branches) which bear large clusters of far longer staminate aments and no pistillate flowers.

"The region where these collections were made is the northern slope of the Cordillera Central between the volcanoes Poas and Barba. Here *Alfaroa* is a common tree between 5000 and 6000 feet above sea level; it attains a height of 80 to 100 feet and possibly more, with trunks two to three feet in diameter. The bark is fairly smooth and varies from light gray to light brown in color. The crown is spreading, with dense compact foliage. It is very beautiful when putting forth new leaves with a delicate light red tint. No one whom I questioned had heard of the name "gaulin." I was given the name "uruca"; but this more properly refers to *Trichilia*. . . ."

"The pistillate spikes are erect; the short staminate catkins stand out from their base. The long staminate catkins from collection 4685 were already so withered when I found them that I can make no definite statement as to their attitude. I should judge they must droop. . . ."

"As the specimens from tree 4684 show, the flowers rise above old leaves much damaged by insects. Since I selected the flowering twigs which bore the best foliage, the majority of the catkins were associated with leaves still more badly worn; hence they arise (on this tree at least) from the tips of old shoots of the previous year. They are terminal (not on lateral spurs) on strong twigs at the very top of the tree. . . ."

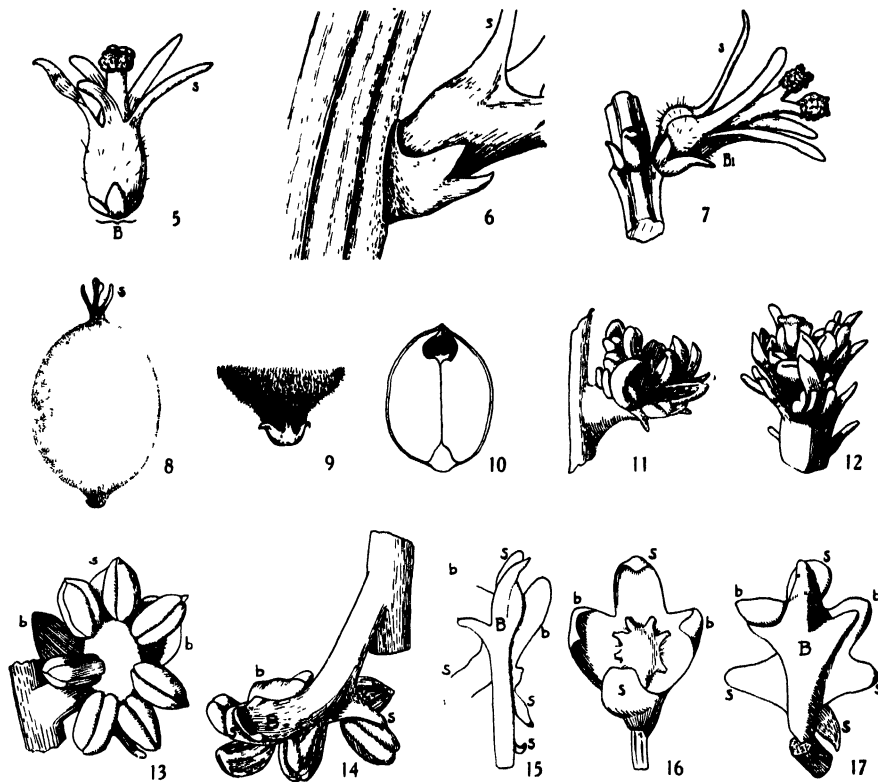
Standley (1927a) describes the staminate flowers as "few, solitary and sessile at the base of the (pistillate) spike or few (2 to 4) and arranged upon two short basal branches." The writer, in his study of the inflorescences (Manning 1938a) stated of the inflorescences of *Alfaroa*, "If the flowers are wind pollinated, as seems probable, the number of staminate flowers is very small, and it is possible that individual branches or individual trees may produce longer staminate catkins. Such catkins have not as yet been found." Skutch has now found such catkins, and it is evident that there are several different combinations of staminate inflorescences.

There are three types of staminate branches which may occur at the base of the pistillate spike: one-flowered, few-flowered, and many-flowered (figs. 2, 3, 11, 12). Furthermore, in some cases the two kinds of flowers may be distinct, the pistillate spikes and the panicles of elongate staminate catkins occurring on separate twigs of the same tree (fig. 3), or on different trees (fig. 1). It is interesting to note from figure 1 that on one twig most transitional stages in position of the staminate panicles can be found from a characteristic terminal position at the tip of a main leafy shoot to a position at the tip of a rather short essentially leafless branch on the old wood, the latter inflorescences thus appearing short-stalked and axillary, similar to the condition in *Engelhardtia pterocarpa* and *E. spicata*, and approaching the conditions in *Pterocarya*, *Juglans*, and *Carya*. Such stages, transitional from ancestral terminal positions to advanced axillary positions were proposed in the article on inflorescences (Manning 1938 a) as necessary theoretical ancestral intermediates, and they have now been found in one modern species.



FIG. 1. *Alfaroa costaricensis* Standley var. *elongata* Manning, var. nov.; Skutch 4685, staminate flowers only; complete catkins of only one panicle drawn, tips of others cut off; panicles terminal on new growth, and in some cases essentially axillary on old growth  $\times \frac{1}{2}$ . FIGS. 2-4. *Alfaroa costaricensis* Standley  $\times \frac{1}{2}$ . FIG. 2. Standley 33620 (TYPE) showing short staminate branches. FIG. 3. Preserved material, collected by Skutch (presumably his 4684), showing panicle of elongate staminate catkins and androgynous panicle (pistillate and staminate catkins) on adjacent branchlets. FIG. 4. Portion of twig with leaf; Skutch 4684.

The internal structure of the fruit was not fully understood by Standley. Better material of *Alfaroa costaricensis* and more detailed study of *Engelhardtia pterocarpa* and *E. mexicana* show that in internal structure of the fruit these three are practically identical. The fruit (figs. 8-10, 18-23) is eight-celled in the middle, owing to the presence of primary, secondary,



FIGS. 5-15. *Alfaroa costaricensis* Standley. FIGS. 16, 17. *Alfaroa costaricensis* var. *elongata* Manning. B, bract; Bl, central lobe of bract; b, b, bracteoles; s, sepal. FIGS. 5, 7. Pistillate flowers; Standley 33620. FIG. 5. The unusual type of flower with 5 sepals, front view. FIG. 7. The usual type, side view. FIG. 6. Base of pistillate flower, side view, much enlarged (Skutch 4684), showing the bracteole rim. FIG. 8. Fruit.  $\times 1$ . FIG. 9. Base of fruit, enlarged. FIG. 10. One valve of nut, showing the small common cavity of the loculus. FIGS. 11, 12. One-flowered staminate branches, without and with central abortive pistil; Standley 33620.  $\times 5$ . FIGS. 13, 14. Staminate flowers stalked, with round receptacles; Skutch 4684. FIG. 15. Staminate flower; Standley 33620. FIGS. 16, 17. Staminate flowers, sessile with elongate receptacles; Skutch 4685.

and tertiary septa. In addition to these there are plate-like outgrowths, lamellae, from the secondary and tertiary septa, these sometimes T-shaped at the ends, thus making the internal structure quite complex—incompletely sixteen-celled; the lamellae disappear toward the base of the fruits. The

tertiaries disappear above, so that the nut is four-celled just below the one-celled apex; the tertiaryes may also be lacking at the very base in those fruits of *Alfaroa* which have tapering bases. Some of the septa or lamellae may be lacking or fused with other septa, so that the internal structure is not uniform in all nuts. The fruits of *Alfaroa* found in most herbaria (*Standley & Torres 50870, 50986*) are unripe ones, in which some of the septa have been pulled apart and distorted by drying. A three-carpelled fruit collected by Skutch has some of the lamellae and septa fused with others, so the fruit is fewer than twelve-celled in the middle. Standley (1927b) described the cross section of the nut of *Engelhardtia mexicana* accurately in his description of that species. The cross-sectional drawing of the similar fruit of *Oreamunoa*<sup>2</sup> *peterocarpa* Oerst. [*E. pterocarpa* (Oerst.) Standl.] by Oersted (1870) was probably of a section taken above the middle, since the nut is shown as only four-celled with the lamellae well developed. Eichler (1878) copied the drawing but numbered the partitions incorrectly.

The wall of the nut is of a different texture from that of *Juglans*, *Pterocarya*, and *Carya*; although it is hard it does not require a saw, but can be cut when wet, though with difficulty, with a heavy razor blade, using a sawing motion. It can be described as subligneous, as opposed to truly woody. The outer fleshy layer of the fruit is much thinner than in *Juglans*, and does not represent ripened bract, bracteole, and calyx tissue as in *Juglans* and *Carya*, but ripened calyx tissue only since the bract and bracteoles remain very small at the base of the fruit.

The dehiscence of the fruit at the time of germination of the seed is along the secondary partition, hence is clearly loculicidal, as is shown by old fruits found on the ground by Skutch (fig. 10).

The leaves vary from alternate to opposite and whorled (figs. 1-4), all three arrangements sometimes occurring on the same twig. The common arrangement seems to be opposite.

As the writer stated in a previous article (Manning 1940) the bracteoles appear absent from the pistillate flower. In some flowers of the abundant preserved material collected by Skutch, there is a minute bracteolar rim around the base of the ovary connected with the side lobes of the bract (fig. 6). In most flowers this rim is buried in the axis of the catkin. The pres-

<sup>2</sup> It is necessary to stabilize the spelling of the generic, sectional, and specific name, *Oreamunoa*. Four different spellings occur in literature. The genus was dedicated by Oersted (1856) to Don Francisco Maria Oreamuno. Unfortunately, in the original description of the genus, Oersted spelled the name of the Costa Rican statesman Oreomunna, and called the genus *Oreomunnea*. Oersted in a book dedicated to Oreamuno in 1863 correctly spelled the latter's name, and in an article on the Juglandaceae in 1870 changed without comment his own spelling of the genus to *Oreamunoa*.

ence of this bracteolar rim shows the relationship to *Engelhardtia* and other genera. Bracteoles are present in the staminate flowers.

Figures 5-7, 11-17 show the pistillate and staminate flowers. Other floral drawings are given in the papers of the writer cited above.

A corrected description of the genus *Alfaroa* is here given (most of the changes from the original are in the staminate inflorescences, bracts and calyx of the staminate flower, position of stigma, embryo, and cross section of the fruit).

**ALFAROA** Standl. Trees or large shrubs; pith solid; buds superposed, closely glandular-dotted, (naked or valvate-scaly?), often hirsute; leaves probably deciduous (?), mostly opposite, occasionally alternate or whorled, estipulate, pinnate, with no truly terminal leaflet, the leaflets numerous, alternate or opposite, serrate on young trees, entire or nearly so on older trees, glandular-punctate beneath at least on younger leaves, membranaceous; monoecious or partially dioecious, some trees exclusively staminate, others with both pistillate and staminate flowers; flowers in spikes or catkins usually in panicles; pistillate spikes terminal, erect, the flowers numerous, about 30-50, inserted singly, closely sessile; staminate catkins clustered in separate drooping panicles terminal on new growth and also on short essentially leafless shoots on the old wood, the lateral flowering shoots often superposed, or the catkins forming side branches at the base of the pistillate spikes, the staminate catkins and pistillate spikes together constituting a terminal androgynous panicle, the staminate side branches often reduced to 2 or 4 short few-flowered spikes or to solitary apparently sessile flowers or absent; staminate flowers stalked or sessile, the receptacle elongated to nearly round, the 3-lobed bract and two bracteoles fused with the floral receptacle and appearing as part of the floral envelope; true sepals 4, 3, or 2, oblong, obtuse, variable in size and arrangement; stamens 6-10 inserted in a single series about a naked center, or occasionally in the solitary flowers with an ovoid rudiment of an ovary, the filaments nearly obsolete, the anthers 2-celled, glabrous, dehiscent by longitudinal slits; pistillate flowers subtended by a minute 3-lobed bract shorter than the ovary, bracteoles apparently absent or sometimes represented by a minute rim around the base of the ovary, the calyx deeply 4- or rarely 5-lobed, the lobes oblong-linear, as long as the style and stigmas, unequal, obtuse, erect, persistent upon the apex of the fruit, the style shorter than the perianth lobes, bifurcate, the 2 (rarely 3) stigmas carinal, median, subglobose, the verrucose stigmatic areas on the outside of the style branches or covering the tips; fruit oval or obovoid, about 2.5 cm. long, with neither husk nor wings, the skin (probably modified calyx) nearly dry, papery-thin, hairy, indehiscent, adhering closely to the nut proper, the bract a scale at the base of the fruit; nut proper neither ridged nor rugose, with coriaceous-subligneous thin walls, falsely 8-celled, with nearly complete primary, secondary, and tertiary septa, the secondary and tertiary with lamellae projecting into the loculus, 8-celled in the lower half, 4-celled near the apex, 1-celled at the very top; seed 8-lobed, 4-lobed, and entire, following the lobes of the loculus, the lobes of the embryo averaging 1 mm. thick, each cotyledon probably 4-lobed, one cotyledon in each valve (not carpel) of the nut, the cotyledons apparently separate from each



other (so lobes of different cotyledons not entangled together); nature of the seedling as yet unknown; nut at time of germination of the seed loculicidally dehiscent, the valves lateral to the axis.

Standley (1927a) gives a complete description of the single species, *A. costaricensis* Standley; this is accurate except for the staminate inflorescences. The distribution is given there and in the *Flora of Costa Rica* (Standley 1937) for that country. In general, *Alfaroa*, known locally in Costa Rica as *gaulin*, *gavillancillo*, or *uruca*, is common in central Costa Rica in forests near Cartago at an elevation of 1250–1800 meters, in western and central Guatemala, and in western Panama. The following are the definite localities recorded in herbarium material for the typical species.

COSTA RICA: El Muñeco, south of Navarro on the Rio Navarro: *Standley 1925* (CM), *Standley 33501* (US, AA), *33504* (US), *33620* (US, TYPE), *Standley & Torres 50870* (US, AA, CM, GH), *50874* (US), *50986* (US), *51078* (US), *51204* (US), *Stork 2691* (US, CM); La Estrella: *Standley 39217* (US); Alto de la Estrella: *Standley 39122* (US); Juan Vinas: *Lankaster 1922* (US); Santa Clara de Cartago: *Lankaster 1929* (CM); Santa Maria Dota: *Stork 1700* (CM); Turrialba: *Dita Keith 371* (CM); Vara Blanca, north slope of Cordillera Central, between Poas and Barba volcanoes: *Skutch 4684*, (US, CM, NY, MBG, WEM), *4686* (US, CM, WEM); La Palma de San Ramón: *Brenes 6300* (CM). GUATEMALA: Dept. Huehuetenango: Cerro Negro: *Steyermark 51690* (CM); between Xoxlac and Nucapuxlac: *Steyermark 48955* (CM). Dept. Suchitepequez: Volcan Santa Clara: *Steyermark 46832* (CM). Dept. Quezaltenango: between Finca Pirineos and Patzulín: *Standley 86951*, *86967*, *86978*, *86981*, *86985*, *87010* (all CM). PANAMA: Chiriqui-Boquete region: *Von Hagen and Von Hagen 2096* (MBG), *2179* (MBG) (these specimens, collected in 1940, are the first records for Panama of any member of the Juglandaceae).

Flowers appear in early February with possibly others in May, fruit from March to April with possibly another group from July to August.

Standley (1927a) and Skutch have pointed out that *A. costaricensis* is extremely variable, the hairiness of twigs, leaf rachises, and leaflets varying from brown-hirsute to glabrous, the apices of the leaflets from strongly acuminate to acute or even obtuse, and the margins of the leaflets from strongly serrate or dentate to entire. In general the first-mentioned features of each group are characteristic of young growth, or stump sprouts, the second of mature growth. Various combinations and intermediates are to be found between. Thus *Dita Keith 371*, *Skutch 4686* (at Chicago Museum), *Standley 39217*, *Standley & Torres 50874* represent characteristic sterile specimens of young growth. *Brenes 6300*, *Skutch 4686* (the writer's personal herbarium) have hairy twigs and rachises, but the serrate leaflets are entirely glabrous. Characteristic mature flowering specimens, the flowers mostly pistillate, are *Skutch 4684*, *Standley 33620*, and *Lankaster 1922*. *Standley & Torres 50870*, *Standley & Torres 50986*, and *Lankaster 1929* are fruiting, only the last having mature fruit. The other specimens listed represent sterile material in various conditions. It should be stated that identifica-

tion of sterile material is uncertain; some specimens may represent a different species, or might even belong in the genus *Engelhardtia*. The Guatemalan collections especially appear somewhat different.

In all of the specimens listed above either the twigs, rachises, or leaflets are hairy or often all three, and the buds are densely brown-hirsute. *Skutch 4685*, a tree with staminate catkins only, is similar to the above specimens in general leaf type and arrangement, but differs sufficiently in certain respects to warrant describing it as a new variety.

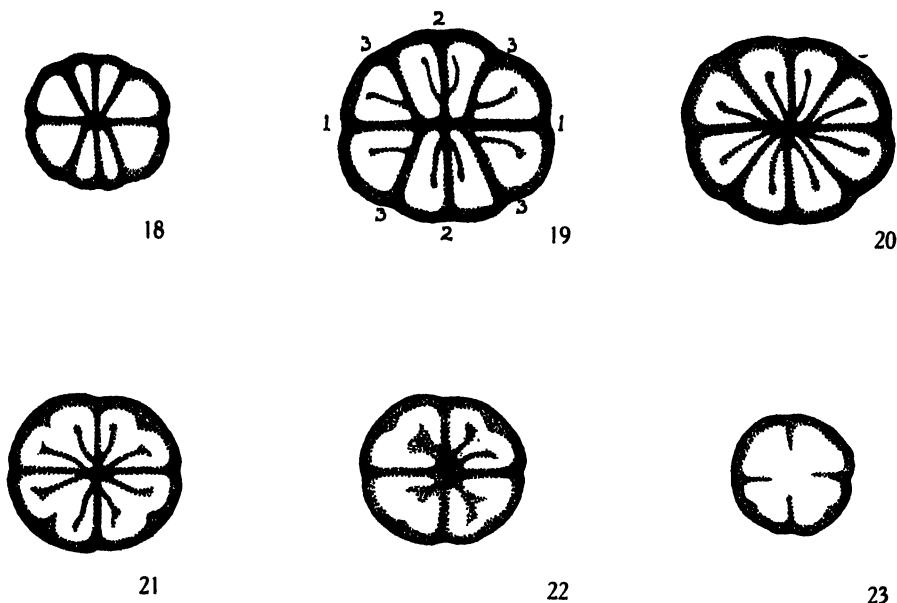
*ALFAROA COSTARICENSIS* var. *elongata* Manning, var. nov. Rhachidibus foliolisque arborum maturorum glabris; foliis petiolatis, petiolo ca. 2 cm. longo; jugis primis foliolorum paullo minoribus quam tertiis vel quartis; amentis staminiferis elongatis, pedulis; florum masculorum receptaculo elongato.

Twigs, rachises, and leaflets absolutely free of hairs; leaves short-petioled; the first leaflets, not so greatly reduced as in typical *A. costaricensis*, with their points of attachments usually 2 cm. (1.5–3.0 cm.) from the stem; leaflets on both sterile and flowering shoots rather narrowly oblong, acute or abruptly acuminate at the apex, obliquely tapering at the base; most of the buds glabrous (only one bud from several specimens having been found with a few brown hairs at its tip); trees apparently dioecious, the slender, greenish, flexible staminate catkins occurring in ample panicles (4–8 catkins each 4–9 cm. long), the panicles terminal on the principal leafy shoots and on short often essentially leafless side shoots located at the tip of the old growth; most of the individual flowers essentially sessile, with receptacles of an elongate type (ellipsoidal to lenticular). TYPE at US: *Skutch 4685*, Vara Blanca, Costa Rica, north slope of Cordillera Central between Poas and Barba volcanoes, February 15, 1940; isotypes at NY, CM, MBG, WEM.

In typical mature *A. costaricensis*, on the other hand, the leaves are essentially sessile, the lowest leaflets much reduced, and usually 1 cm. (0.5–1.5 cm.) from the stem; the leaflets are often oval, obtuse or acute on flowering twigs, abruptly acuminate on sterile shoots, sessile, truncate, or rounded at base; the trees are monoecious, the staminate spikes usually short at the base of the pistillate spikes, only in exceptional cases in separate clusters of about 4–8 long, commonly almost sessile, stoutish, rather stiff brown catkins; the individual flowers, when fully developed as in the long catkins (*Skutch 4684*), are clearly stalked with nearly round receptacles.

The most important features of the variety are the glabrous twigs, rachises, leaflets, buds, the petioled leaves, and the sessile flowers with rather elongate receptacles; the epithet *elongata* refers to the elongate staminate catkins, though it applies equally to other features (petiole, stalk of catkins, receptacle). The specimens drawn were picked to show certain floral features, and do not of course show all characters equally well. Another specimen of *Skutch 4685* had six leaves on the principal shoot, the lower three large and alternate, two of the upper three large, these two and a small one each apparently subtending the lower catkins of the panicle as in *Platycarya*,

*Rhus*, etc. *Standley & Torres 50969* (El Muñeco, US, AA) and *Standley 39446* (La Estrella, US) are sterile representatives of the variety, both with elongate petioles and comparatively long lower leaflets. The former, from a tree 25 feet high, is glabrous throughout with serrate leaflets; the latter has hairy twigs and rachises with entire leaflets and is thus transitional to typical *A. costaricensis*. Trees or branches of the variety with pistillate flowers and fruits may yield other features of difference or of resemblance between the species proper and the variety *elongata*. The fruits from which the cross sections were drawn (figs. 10, 18-23) were picked up from the ground by



FIGS. 18-23. *Alfaroa costaricensis* Standley (exact variety uncertain, but probably not var. *elongata*); cross sections of fruit, arranged from base (fig. 18) to apex (fig. 23), showing primary, secondary, and tertiary septa (1, 2, 3 respectively), with lamellae (plate-like outgrowths from septa) at certain levels.

Skutch, and the nature of the leaves of the tree from which it came is unknown. *Lankaster 1929* has similar fruit.

The differences given above are at the same time striking and intangible. It is both remarkable and significant that the differences between *A. costaricensis* and its variety *elongata* are nearly identical with the differences between *Engelhardtia spicata* and its varieties *aceriflora* and *Colebrookiana* [for many years these were considered distinct species, until Koorders and Valetton (1900) pointed out that all differences fluctuated]. *E. chrysolepis* also varies from monoecious to possibly dioecious and is quite diverse in leaves and fruit.

Standley (1927a) described the genus as closely related to *Juglans*. He stated that *Alfaroa* differed in having opposite leaves, no terminal leaflet, smooth instead of rugose nuts, very short instead of long, drooping staminate catkins. But there are other more fundamental differences which set these two genera apart within the family. *Alfaroa* has staminate catkins in clusters, these typically in terminal inflorescences, often in the same inflorescence with the pistillate spike, the latter many-flowered; the stigmas are short with the stigmatic tissue on the outside covering the tips; the bract is three-lobed in staminate and pistillate flowers, is practically separate from the ovary, and does not form a husk; bracteoles are much reduced or apparently absent in the pistillate flower; in the fruit tertiary septa are present; the pith is solid, not chambered, and the wood has many scalariform perforations in the vessels, not simple ones, with rays of type heterogeneous I, not heterogeneous II B.

*Alfaroa* is more closely related to *Engelhardtia*. This relationship has been indicated in studies on the inflorescences, pistillate and staminate flowers (Manning 1938a, b, 1940, 1948) and on the wood anatomy (Kribs 1927, Heimsch & Wetmore 1939). The flower and fruit features in common between these two genera, many of them indicated in the paragraph above as differences between *Juglans* and *Alfaroa*, are indicated in table 1.

The genus is especially close to the American species of *Engelhardtia*: *E. pterocarpa* (Oersted) Standley (*E. Oreamunoa* DC.), *E. mexicana* Standley, and *E. guatemalensis* Standley. The first species, which was considered by Oersted (1856, 1870) to constitute a genus *Oreamunoa* distinct from the Asiatic species of *Engelhardtia*, was placed by de Candolle (1862, 1864, 1914) in a special section *Oreamunoa* of the genus *Engelhardtia*. Oersted (1870), in his second discussion of the generic characters of *Oreamunoa*, stressed the shape of the stigmas (though he incorrectly described the stigmas of *E. spicata* as always four—see Manning 1940), the four-celled instead of a two-celled condition in the ovary (should be eight-celled instead of two-four-celled), the similarity in the form of the seed to that of the embryo (cotyledons), and the fact that the cotyledons are not entangled but separate from each other though bent and folded. Engler (1889) copied some of the errors of Oersted in his key to the genera. In many ways *Alfaroa costaricensis* seems so close to the American species of *Engelhardtia* that it might be placed as a species in this genus *Oreamunoa*; the internal structure of the fruit, as indicated earlier, is almost identical; other features in common are shown in the table.

The decision on whether to recognize *Oreamunoa* or *Alfaroa* depends upon which criteria, of the many similarities and differences that can be given, one should emphasize. Studies of the inflorescences and flowers have shown that many distinguishing characters vary tremendously within a



TABLE 1. Comparison of *Alfaroa* with certain genera and species.—(Cont'd.)

	<i>Alfaroa</i>	<i>Engelhardtia pterocarpa</i>	<i>Engelhardtia mexicana</i>	<i>Engelhardtia chrysolepis</i>	<i>Engelhardtia spicata</i>	<i>Juglans</i>	<i>Pterocarya</i>
Stigmas	carinal	carinal	carinal	split- carinal	commissural	carinal	carinal
Stigmatic area	short round	short round	short round	short hidden	long	long	long
Fruiting bract	scale	3 wings	3 wings	3 wings	3 wings	fleshy husk (narrow)	scale
Fruiting bracteoles	scale	small wing	small wing	small wing	small wing	large fleshy husk	2 large wings
True husk	absent	absent	absent	absent	absent	present	absent
Tertiary septa	present	present	present	absent	absent	absent	absent
Cotyledons (in fruit)	separate	separate	†	entangled	entangled	separate	entangled
Cotyledon (at germination)	†	†	†	epigaeous	epigaeous	hypogaeous	epigaeous
Fruit (ovary)	hairy	glabrous	glabrous	glabrous	hairy	hairy	glabrous
Nut	smooth	smooth	smooth	smooth	smooth	ridged	ridged
Fruit (nut)	large	medium	small	very small	very small	large	small

genus, especially *Engelhardtia*, and it is difficult to choose true generic criteria. It is clear that the only reliable features are the position in flower and the condition in fruit of the bract and bracteoles (prophylls), associated with similar calyx, carpel, and inflorescence characters.

On these bases *Oreamunoa* is not a good genus, and *Alfaroa* should be recognized. The species of the genus *Oreamunoa* proposed by Oersted and the Asiatic species of *Engelhardtia* are held together in the latter genus by having, as shown in table 1, identical sepal, carpel, and inflorescence features, and a three-lobed bract united with only the lower half of the ovary and much enlarged in fruit for wind dissemination; the body of the fruit (the nut) is relatively small, too (up to 1 cm. long), that of *E. mexicana* forming the connecting link between the very small Asiatic and the larger American forms; *E. mexicana* is also intermediate in its stigma size between *E. chrysolepis* and *E. pterocarpa* (see figures in Manning 1940).

*Alfaroa* differs from all other genera in the *Juglandaceae* in having neither bract nor bracteoles specialized in fruit; thus its fruiting bract is very small, a scale at the base of the nut, and the bracteoles even more reduced, so that the fruit has neither true husk nor wings; its relatively large nut (over 2 cm. long) is associated with a type of dissemination other than the wind. Occasional abnormal (?) regular-sized fruits of *Engelhardtia chrysolepis* with the fruiting bract remaining small (this form called *E. fenzelii* by Merrill) show how the small bract of *Alfaroa* might have arisen. The apparent absence or great reduction of bracteoles in the pistillate flowers and fruit is associated with the closely sessile flower. The genus *Alfaroa* differs also from other genera in having in some inflorescences one-few-flowered staminate spikes, but these merely represent stages in the complete separation of pistillate and staminate catkins, a condition present in many members of the family. Other features of leaflets, inflorescences, pistillate flowers, fruits and stamens, separating *Alfaroa* from *Engelhardtia pterocarpa* and *E. mexicana*, constituting the proposed genus *Oreamunoa* of Oersted, are indicated in the table. *Alfaroa*, though a weak genus closely related to *Engelhardtia* sect. *Oreamunoa*, is as distinct from *Engelhardtia* as *Juglans* is from *Pterocarya*, where the real critical differences are in the position in flower and the condition in fruit of the bract and bracteoles.

*Alfaroa* is a very primitive member of the *Juglandaceae*; its primitive features are in its stigmas, calyx, fruit structure, inflorescence type and position, and wood anatomy; its staminate flowers are somewhat advanced. *Alfaroa* and *Engelhardtia pterocarpa* have sprung from a common ancestor.

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NOTE: Since the above was sent to press, an excellent article on the *Juglandaceae* and other families by Dr. Hakon Hjelmqvist has appeared ["Studies on the floral

morphology and phylogeny of the Amentiferae'' (Bot. Not. Suppl. 21: 1-171. 1948)]. Dr. Hjelmqvist adopts a different interpretation for the floral parts of various members of the Juglandaceae, including *Alfaroa*, considering the three-lobed bract in both staminate and pistillate flowers of this genus as a bract and two bracteoles; he illustrates the cross-section of the fruit of *Alfaroa* as only 4-celled, and erroneously interprets the stigmas as commissural; the genus *Oreomunnea* (*Oreamunoa*) is recognized, and the inflorescence of *O. pterocarpa* (*Engelhardtia pterocarpa*) is shown to be terminal on the main shoots, not lateral.

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## A NEW SPECIES OF CARLUDOVICA (CYCLANTHACEAE) FROM SOUTHERN MEXICO

EIZI MATUDA

*Carludovica chiapensis* Matuda, sp. nov. Planta epiphytica scandens cum radicibus adventitiis, caudice crasso dense 3-5 cm. diam.; folia magna longipetiolata, coriacea et fibrosa; petiolo 65-75 cm. longo ca.  $\frac{1}{2}$  longitudine vaginato, lamina basi acute attenuata 70 cm. longa medio ca. 30-35 cm. lata apicem versus ca.  $\frac{1}{2}$  longitudine bifida a segmentis 15-17 latis apicem acutis, 14-vel 16-nervatis; pedunculis 15-20 cm. longis crassis, in vivo striatis; spatharum nodis 6, albidis, concavis, 10-15 cm. longis, deciduis; spadice simplicis, in vivo cylindrico 6-8 cm. longo, 1.5-2 cm. diam. apice rotundato; floribus femineis parvis conerescentibus ca. 1.5 mm. diam.; perianthio saepe 4-lobato, lobis rotundatis, stigmatibus sessilibus parvis ca. 1 mm. diam. in apicem ovarii confluentibus cruciformibus; floribus masculis parvis ca. 3 mm. diam. perianthio inaequali 6 lobato, lobis acutis; staminibus numerosis, filamentis brevibus, antheris oblongis bilocularibus; staminodiis luteis filiformibus, deciduis, 15-20 cm. longis, in floribus femineis 4 perianthio et stigmate interjectis.

MEXICO: Chiapas: Finca Corcega, about 14 km. northeast of Pueblo Nuevo Comaltitlan (a Pan-American Railway Station), on wet mixed forest, at 900 m. altitude, April 19, 1948, *Matuda 17694*; type in Matuda Herbarium, isotypes in the Instituto de Biología of Mexico, Museo de Dirección General de Agricultura of Mexico, and the Chicago Natural History Museum. Local name: "Tepejilote."

*C. latifrons* Drude, apparently is closely related, but the larger leaves and 6 spathes amply distinguish *C. chiapensis* from that Brazilian species. Another affinity is with *C. utilis* of Costa Rica, but from this our species with its deciduous spathes and larger leaf can be separated readily. As far as I am aware, this is the first record of the genus from Chiapas. The only other Mexican record we have is *C. gracilis* from Oaxaca. All descriptions hitherto published in the genus are deficient in their characterization of the very small floral organs. Fortunately I have secured sufficient fresh material of the present species and it was possible to observe all the characters of these floral structures. The surface of the spadix is covered with numerous long staminodes and the staminate flowers contain numerous oblong anthers as shown in figure 2. Figure 3 shows pistillate flowers after the staminodes and staminate flowers were carefully removed, leaving only their vestiges. The male flowers are practically located two by two vertically. The 6-lobed perianth is developed only at the outside of the pair of flowers as shown in figure 7; the inner side is entirely destitute of perianth. It is possible to say that one female flower is surrounded by eight

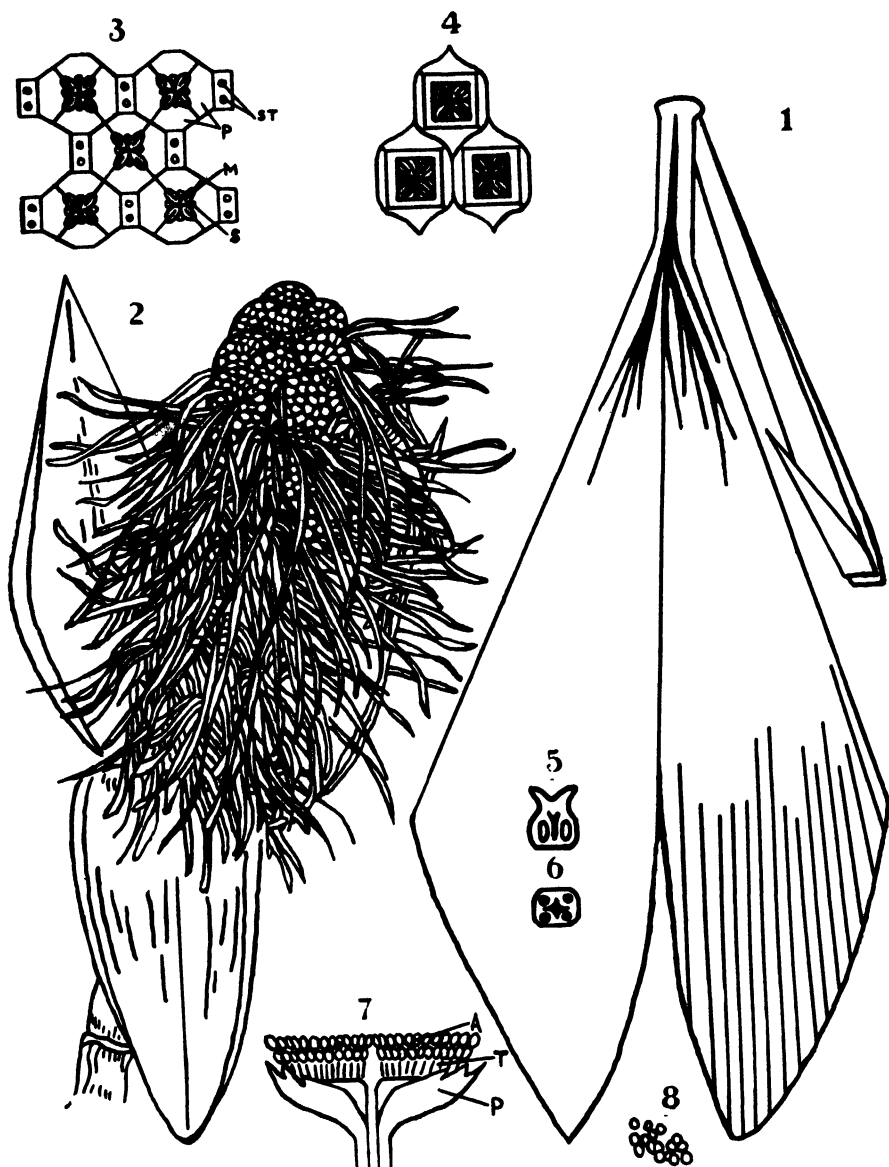


FIG. 1. General aspect of leaf.  $\times \frac{1}{6}$ . FIG. 2. General aspect of mature flower opened.  $\times 1$ . In the upper part of the spadix the staminodes are already fallen, exposing the concourse of anthers. Upper three spathes shown. Staminodes cut lengthwise. FIG. 3. Female flowers covering the spadix, exposed by removal of male flowers and staminodes.  $\times 5$ . M, cruciform stigma. P, perianth. S, vestige of staminodes, four in each female flower. St, vestige of male flower, showing two vertical colocations. FIG. 4. Surface of spadix when fruits are ripe. Stigma and perianth also developed, greenish-yellow. Stigma and perianth fallen, exposing juicy yellow naked fruits which contain 4-12 small, thin, oblong seeds. Length of seed approximately 0.5 mm. FIG. 5. Female flower, vertical section.  $\times 4$ . FIG. 6. The same, horizontal section of ovary.  $\times 4$ . FIG. 7. Pair of male flowers.  $\times 6$ . P, perianth. A, anthers. F, filaments. FIG. 8. Pollen.  $\times 80$ .

male flowers, two in each direction, or to say that two males are surrounded by four females, one in each direction (fig. 3). This is the essential difference between *C. chiapensis* and all other species of the genus. In the other species, as Wettstein has pointed out, "one female flower is surrounded by four male flowers." On a single spadix the male flowers ripen first and the female flowers 7-10 days later. When the female flower is mature a colorless gum-like fluid is secreted on the stigma which attracts insects. The pollination seems to be accomplished by insects. On the blade of a segment of the leaf there are 14 or 16 semipalmate and semiparallel veins conspicuously separate and alternate on both surfaces. Immature spadices covered closely by the spathes are cooked by local natives. They erroneously regard these young flowers as fruits, saying "Fruta tierna se come." These spadices are said to be very bitter so that one needs to renew the water three times in boiling them. After being thoroughly boiled they are usually fried with eggs in the same way as the so-called "Pacaya" (the young flower of *Chamaedorea* spp. in their sheaths) which in Oaxaca is generally known as "Tepejilote" according to Standley. In his "Flora of Costa Rica" Standley says, "Oersted states that the Indians ate the ripe spadices, like those of *C. utilis*, but I have never heard mention of the edible quality of the fruits, so it is possible that they are no longer eaten." It is not known whether the stalk, leaves and adventitious roots are used locally.

It is my pleasant duty to acknowledge the many favors and friendly suggestions made by Dr. Harold N. Moldenke of the New York Botanical Garden in preparation of this paper.

MATUDA HERBARIUM

ESCUINTLA, CHIAPAS.



gand & Eames 1926). The species "shows a wide acidity tolerance and is found in acid and alkaline regions alike. It is very often found in association with *Anopheles quadrimaculatus* and in some instances constitutes a major problem" (Eyles & Robertson 1944). It has become a pest in some of the reservoirs constructed by the Tennessee Valley Authority (Hall 1940). Its

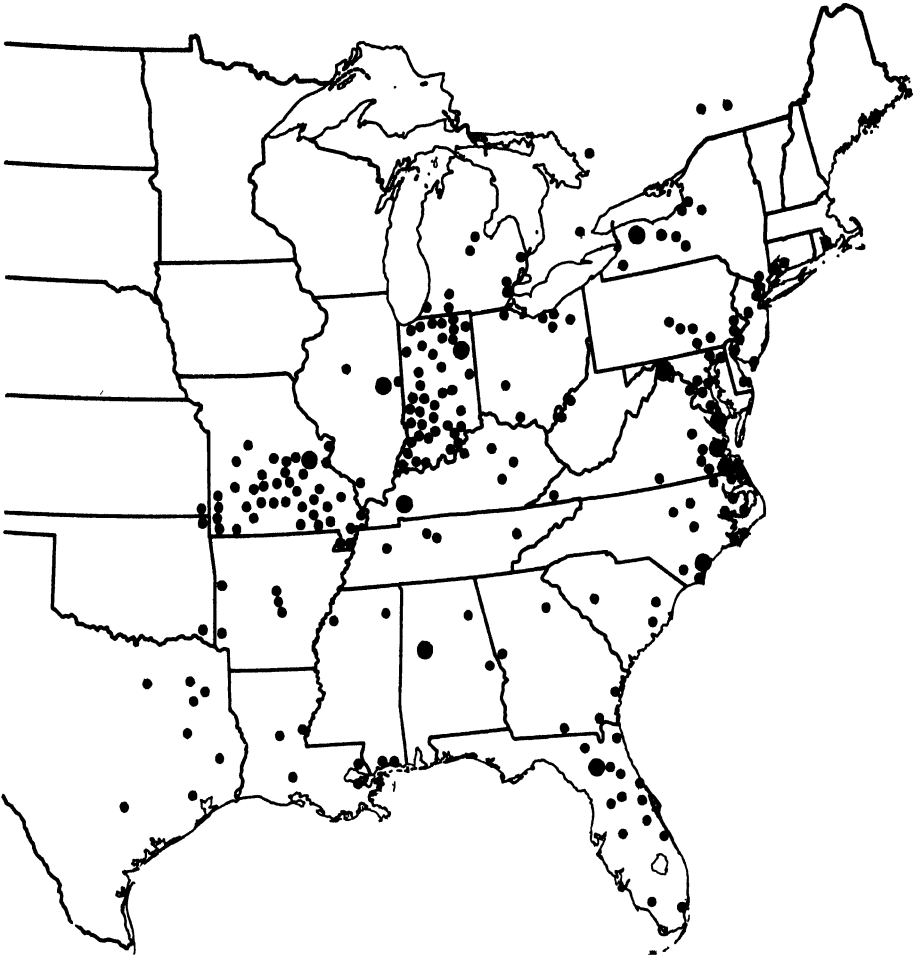


FIG. 1. Distribution of *Saururus cernuus*. Small circles indicate herbarium and literature records; big circles show origin of plants cytologically examined.

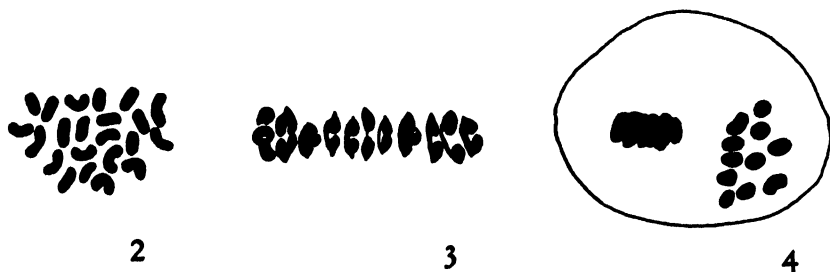
populations vary in size from a few individuals to millions. It readily propagates itself both by vegetative means and by seed. Hall (1940) estimated that about twenty thousand seed per square foot of colony of *Saururus* are produced each year.

This plant has a  $2n$ -number of 22,  $n$ -number of 11 (figs. 2-4). Propio-

carmine smears of very young leaves evidenced many mitoses and were good for study. Smears of pollen mother-cells were especially clear, and all meiotic stages were found in the anthers of a single flower. This material would be excellent for class use. From hematoxylin preparations of microsporogenesis Täckholm and Söderberg (1918) determined the  $n$ -number of this species to be 10.

*Saururus chinensis* (Lour.) Baill. is the only other representative of the genus. We have seen herbarium specimens from Japan, Formosa, south-eastern China, French Indo-China, and the Philippines. Seemingly the chromosomes have not been investigated.

*Houttuynia* Thunb., with one species in Japan, China, and the Himalaya region (Söderberg 1927), and *Anemopsis* Hook., with one species from New Mexico to southern Utah, Nevada, and southern California to Mexico (Tidestrom & Kittell 1941), are closely related to *Saururus*. These three genera and four species are referred by some authors to the family Saururaceae



FIGS. 2-4. Chromosomes of *Saururus cernuus*. FIG. 2. Mitotic metaphase from leaf. FIG. 3. Metaphase I of microsporogenesis. FIG. 4. Metaphase II of microsporogenesis. Magnification  $\times 2200$ .

and by others to the tribe Saurureae of the Piperaceae. In having three or four free or united carpels with two or more non-basal ovules these genera stand apart from the Piperaceae proper, which have a one-celled ovary with a single basal ovule (Rendle 1938). And there are likewise marked differences in vascular tissue (Solereder 1908).

Shibata and Miyake (1908) reported *Houttuynia cordata* Thunb. to be parthenogenetic, with abortive pollen and with a  $2n$ -number of 52-56. Söderberg (1927) questioned the existence of apogamy in this plant and recorded that  $2n = 100-104$ ,  $n = \text{ca. } 50$ . Okabe (1930) arrived at a  $2n$ -number of 94-98 and discovered meiosis to be irregular at both micro- and megasporogenesis, but in some cases the megaspore mother-cell exhibited only univalents with resultant diploid embryo-sacs which developed parthenogenetically. According to one of Tischler's chromosome lists Okabe in 1934 reported the  $2n$ -number of this species to be ca. 96.

The chromosomes of *Anemopsis californica* (Nutt.) Hook. and Arn. have not been examined.

As living plants for the other three species of this complex come to hand, we plan to investigate them for chromosomal comparison with *Saururus cernuus*.

#### SUMMARY

*Saururus cernuus* has a geographic range from Montreal, Quebec, to Texas and to Florida. It often forms extensive colonies affording excellent breeding places for anopheline mosquitoes, and, for that reason, the plant is considered a pest.

Chromosome counts for plants from twelve localities have been made:  $2n = 22$ ,  $n = 11$ . An  $n$ -number of 10 has been reported by other workers.

*Saururus* likewise has a species in Asia. *Houttuynia* is a related monotypic genus in Asia; for it differing chromosome numbers and conflicting accounts of parthenogenesis are in the literature. *Anemopsis* is a second monotypic genus showing affinity to *Saururus*; it is in the southwestern United States and adjacent Mexico. Some authors refer these four species in three genera to the family Saururaceae; others, to the tribe Saurureae of the Piperaceae.

COLLEGE OF WILLIAM AND MARY  
WILLIAMSBURG, VIRGINIA

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## TORREYA

**Arthur Dobbs (1750) and the Discovery of the Pollination of Flowers by Insects.**

It is stated in all historical accounts of the subject that Joseph Gottlieb Kölreuter was the first to point out that insect visits are necessary for the pollination of flowers.<sup>1</sup> Kölreuter himself apparently regarded his discovery as unprecedented, for he exclaims that: "Gewiss, ein ieder anderer, der vor mir diese Betrachtungen angestellt hätte, würde sie längst entdeckt, und sich und allen Naturforschern von diesem Geheimnisse der Natur den Vorhang weggezogen haben."<sup>2</sup> As it happens "ein ieder anderer" had indeed already discovered that flowers are pollinated by bees and had communicated this observation to the Royal Society of London in 1750. It cannot diminish the fame of Kölreuter, whose greatness really consisted in his experimental approach to sexuality and hybridization in plants, to record at this belated date the contributions of a certain Arthur Dobbs in Ireland.

Having perused the entomological memoirs of M. de Réaumur<sup>3</sup>, Mr. Dobbs finds that he differs from that authority on two particulars. Réaumur has stated that wax is formed internally in bees and is discharged through the mouth, whereas Dobbs has observed it to be excreted through the anus. Furthermore, the French naturalist claims that bees roam from the flowers of one species of plant to those of another species while gathering pollen, and this Dobbs denies. Addressing himself to the Royal Society, Arthur Dobbs discourses as follows:

"As to the [latter point in which I differ from M. *Reaumur*], I have frequently follow'd a Bee loading the *Farina*, Bee-Bread, or crude Wax, upon its Legs, through a Part of a great Field in Flower; and upon whatsoever Flower I saw it first alight and gather the *Farina*, it continued gathering from that Kind of Flower; and has pass'd over many other Species of Flowers, tho' very numerous in the Field, without alighting upon or loading from them; tho' the Flower it chose was much scarcer in the Field than the others: So that if it began to load from a Daisy, it continued loading from them, neglecting Clover, Honeysuckles, Violets, &c.; and if it began with any of the others, it continued loading from the same Kind, passing over the Daisy. So in a Garden upon my Wall-Trees, I have seen it load from a Peach, and pass over Apricots, Plums, Cherries, &c. yet made no Distinction betwixt a Peach and an Almond.

"Now M. *Reaumur*, in his Memoir upon the Bee's making Honey, mentions *Aristotle's* Observation of the Bee's loading or gathering from one Species of Flower without changing; not quitting a Violet to gather from a Cowslip; which he says is not justly founded; for he has observed frequently a Bee on a large Border gathering from Flowers of different Species. If M. *Reaumur* only means, that, when the Bee gathers Honey, it takes it indifferently from any Flower, I can say nothing against it; but, if he intends it to mean the Bee's loading the *Farina* upon its Legs, then my Observation directly contradicts it.

"What further confirms my Observation is this, that each Load upon the Legs of a Bee is of one uniform Colour throughout, as a light Red, an Orange, a Yellow, a White, or a Green, and is not upon different Parts of the Load of a different Colour; so that as the *Farina* of each Species of Flowers, when collected together, is of one uniform Colour, the Presumption is, that it is gather'd from one Species. For, if from different Kinds, Part of the Load might be of one Colour, and Part of another.

"Another Observation to confirm the same Fact is, that Bees, in the Height of the Season, return to their Hives with Loads of very different Magnitudes, some having Loads as great as small Shot, whilst others have very small Loads; it cannot be conceiv'd that

<sup>1</sup> Müller, H. The fertilization of flowers. 1883. [transl. D'Arcy Thompson, London.]  
 Sachs, J. History of botany (1530-1860). 1890. [transl. H. E. F. Garney, Oxford.]  
 Knuth, P. Handbook of flower pollination. 1906. [Transl. A. Davis, Oxford.]  
 Norden-skiöld, E. The history of biology. New York and London, 1928. Reed, H. S. A short history of the plant sciences. Waltham, Mass., 1942.

<sup>2</sup> Kölreuter, J. G. Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen. Leipzig, 1761-1766.

<sup>3</sup> Réaumur, M. de. Mémoire pour servir à l'histoire des insectes. Paris, 1740. [vol. 5.]



this Difference is from the Inactivity or Sloth of the Bee in collecting its Load, but rather from the Scarcity of the Flowers, upon which it first began to Load.

"Now, if the Facts are so, and my Observations true, I think that Providence has appointed the Bee to be very instrumental in promoting the Increase of Vegetables; but otherwise, might be very detrimental to their Propagation; and at the same time they contribute to the Health and Life of their own Species.

"From the late Improvement made by Glasses, and Experiments made, in observing the Works of Nature, it is almost demonstrable, that the *Farina* upon the *Apices* of Flowers is the Male Seed; which entering the *Pistillum* or *Matrix* in the Flower, impregnates the *Ovum*, and makes it prolific. . . Now, if the *Farina* of specifically different Flowers should take the Place of its own proper *Farina* in the *Pistillum*, like an unnatural Coition in the animal World, either no Generation would happen, or a monstrous one, or an Individual not capable of further Generation.

"Now if the Bee is appointed by Providence to go only, at each Loading, to Flowers of the same Species, as the abundant *Farina* often covers the whole Bee, as well as what it loads upon its Legs, it carries the *Farina* from Flower to Flower, and by its walking upon the *Pistillum* and Agitation of its Wings, it contributes greatly to the *Farina's* entering into the *Pistillum*, and at the same time prevents the heterogeneous Mixture of the *Farina* of different Flowers with it; which, if it stray'd from Flower to Flower at random, it would carry to Flowers of a different Species."<sup>4</sup>

We may set the foregoing statements of Dobbs against the historical background. In 1694 Rudolf Jacob Camerarius<sup>5</sup> had demonstrated experimentally the existence of sexual reproduction in plants. The question which next arose was how, in the natural course of events, the pollen is conveyed from the anthers to the stigmas. That question was answered some years later in Germany by Kölreuter, who explained that some flowers are pollinated by insects and others by wind. Christian Konrad Sprengel subsequently revealed that the true role of insects was to convey pollen from one flower to the stigmas of another flower, since: "die Natur [scheint] es nicht haben zu wollen, dass irgend eine Blume durch ihren eigenen Staub befruchtet werden soll."<sup>6</sup> The biological significance of this emphasis on cross-pollination in the plant kingdom was first perceived by William Herbert, who noted that the progeny of artificial outcrosses of *Hippeastrum* were more vigorous than seedlings derived from self-fertilizations.<sup>7</sup> Darwin, taking the matter up at this point, announced the generalization (really an erroneous overgeneralization as it later turned out) that nature "abhors perpetual self-fertilisation."<sup>8</sup> Such in outline is the development, by the first experimental geneticists, of the doctrine of sexuality in plants.

The observations and deductions of the Irish amateur, when viewed in the time scale, outrange those of the earliest geneticists at both ends. To begin with, he has repeated and confirmed the ancient observation of Aristotle<sup>9</sup> to the effect that bees remain constant to one kind of flower at a time; and he has correctly noted that the flower constancy of bees is more rigorous when they are gathering pollen than when they are taking nectar. These facts were not revived again, so far as I have been able to learn, until the time of Darwin.<sup>10</sup> The lines of evidence which Dobbs adduces in support of the thesis of flower con-

<sup>4</sup> See the list of Dobbs' titles at the end of this paper. The quotation is from p. 538-540 of the last paper.

<sup>5</sup> Camerarius, R. J. De sexu plantarum epistola. 1694. [transl. M. Möbius in Ostwald's Klassiker, Leipzig, 1899.]

<sup>6</sup> Sprengel, C. K. Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen. Berlin, 1793. [p. 56.]

<sup>7</sup> Gärtner, C. F. Versuche und Beobachtungen über die Befruchtungsorgane der vollkommeneren Gewächse und über die natürliche und künstliche Befruchtung durch den eigenen Pollen. Stuttgart, 1844. Knight, T. A. An account of some experiments on the fecundation of vegetables. Philos. Trans. Roy. Soc. 89: 195-204. 1799. Herbert, W. Amaryllidaceae; preceded by an attempt to arrange the monocotyledonous orders and followed by a treatise on crossbred vegetables, and supplement. London, 1837.

<sup>8</sup> Darwin, C. The various contrivances by which orchids are fertilised by insects. London, 1862. [ch. 9.]

<sup>9</sup> Aristoteles. Historia animalium. [Transl. D'Arcy Thompson, Oxford, 1910; bk. 9, ch. 40, p. 624b.]

<sup>10</sup> Darwin, C. The effects of cross and self fertilisation in the vegetable kingdom. London, 1876. [ch. 11.] Bennett, A. W. On the fertilisation of certain Labiatae. Nature 10: 92, 93. 1874.

stancy have a modern ring; the examination of the pollen loads of bees for the purpose of estimating the fidelity of their visits to one kind of flower is a technique which is being used currently (for example, Brittain and Newton in 1933<sup>11</sup>).

With regard to the manner of the pollination of flowers by bees, Dobbs has brought out two conclusions of great importance: first, bees carry the pollen from one plant to another of the same species, and so effect cross-fertilization; secondly, they do not take the pollen from the flowers of one species to those of another, and, to the extent that they do not, they prevent interspecific hybridization. Darwin, who knew of Dobbs' work and cited it, understood very well the first fact, but appears to have missed entirely the significance of the second deduction. "That insects should visit the flowers of the same species as long as they can, is of great importance to the plant, as it favors the cross-fertilisation of distinct individuals of the same species," he wrote in 1876 (ch. 11); but he did not add: and it also prevents the cross-pollination of individuals belonging to different species. The latter deduction pertained to an aspect of pollination studies that was not being emphasized just then. It was not indeed until 1947, when Mather published some experimental results relevant to the species problem in *Antirrhinum*, that anyone seems to have given much thought to the possibility, suggested by Dobbs in 1750, that the flower constancy of bees might operate in nature as an isolating mechanism.<sup>12</sup>

I have gathered little biographical information on Arthur Dobbs, preferring to leave that task for the historian of science. He lived at Castle-Dobbs on the northeast coast of Ireland, near Carrickfergus in the County of Antrim. A list of his contributions to the Royal Society is given at the end of this article. Dobbs was both a careful and a well-informed observer of astronomical phenomena. With regard to the geography of the North Pacific area Dobbs disagrees with Captain Behring that the coast sighted by the latter navigator east of Kamschatka is mainland joined with California, holding it rather to be a great island. His comments on this point are revealing, for they connect him with the search for a Northwest Passage. He speaks as though he has personally "promoted . . . the Attempt . . . [to] sail through" (i.e., from Hudson's Bay to the Pacific Ocean). "A few Months now, if our Ships return safe, will give us a Certainty on one Side or the other . . ." This was in 1747. Three years later (1750) he has his certainty and writes: "Since my View of doing Good, by making Discoveries of the Great World has been disappointed, upon my Retirement into this little Corner of it (*Ireland*) amongst other rural Amusements I have been contemplating the Inhabitants of the Little World; particularly that most useful and industrious Society of Bees."

In conclusion, an Irish country squire and amateur naturalist by the name of Arthur Dobbs published in 1750 some significant observations and deductions concerning the mutual relationships of flowers and bees. Dobbs preceded Kölreuter by a decade in the discovery that bees effect the pollination of flowers, Sprengel by some forty-three years in the conclusion that the activities of the bees cause the flowers to be cross-pollinated; he anticipated Darwin by a century in linking cross-pollination to the flower constant habits of bees, and preceded Mather and the present author by two centuries in pointing out how the flower constancy of bees might operate as an isolating mechanism.—Verne Grant.

**Dobbs, A.** 1722. An account of a parhelion, seen in Ireland. *Philos. Trans. Roy. Soc.* 32: 89-92.

———. 1726. An account of an aurora borealis seen in Ireland in September 1725. *Philos. Trans. Roy. Soc.* 34: 128-132.

———. 1729. An observation of the eclipse of the moon at Castle-Dobbs near Carrickfergus in Ireland, Feb. the 2d, 1728-9. *Philos. Trans. Roy. Soc.* 36: 140, 141.

———. 1747. Concerning the distances between Asia and America. *Philos. Trans. Roy. Soc.* 44: 471-476.

———. 1750. Concerning bees, and their method of gathering wax and honey. *Philos. Trans. Roy. Soc.* 46: 536-549.

<sup>11</sup> Brittain, W. H. & Newton, D. E. A study of the relative constancy of hive bees and wild bees in pollen gathering. *Canad. Jour. Res.* 9: 334-349. 1933.

<sup>12</sup> Mather, K. Species crosses in *Antirrhinum*. I. Genetic isolation of the species *majus*, *glutinosa* and *orontium*. *Heredity* 1: 175-186. 1947. Grant, V. Pollination systems as isolating mechanisms in angiosperms. *Evolution* 3: [in press].

## REVIEWS

**The Flowers that Bloom in the Spring in Rockland County.** By John M. Price. The Rockland Audubon Society, West Nyack, N. Y.

This is a set of six mimeographed sheets making a calendar which lists 144 spring flowers in a table, with the dates of first bloom, the colors, and likely locations. There is a blank column left for the user to list his own first dates. Included are notes on using the calendar, on botanical names, on picking flowers, and on useful flower guides. The work is priced at 15 cents each or \$1.00 for ten. It should be a useful model for school projects elsewhere.—T. C. R.

**Check-List of the Vascular Plants of Maine.** By E. C. Ogden, F. H. Steinmetz and F. Hyland. Bulletin of the Josselyn Botanical Society of Maine, Number 8. August, 1948.

This is a pamphlet of 70 pages reproduced by photooffset from typewritten copy. It lists by families the species of vascular plants found in Maine, with check-marks showing their distribution by counties. The nomenclature is essentially that of *Gray's Manual*, with, however, many corrections due to recent research. The list is based on a painstaking and systematic keeping of records which extends back through many years, and should be of great value for future students of the flora of Maine.

The book may be obtained through Dr. F. H. Steinmetz, Coburn Hall, University of Maine, Orono, for 50 cents prepaid.—H. W. R.

## PROCEEDINGS OF THE CLUB

**Minutes of the meeting of January 19, 1949.** The meeting was called to order by President Matzke at Hunter College at 8:10 P.M.; 20 members and friends were present. The minutes of the annual meeting were read and approved.

The president reported that the petition authorized at the last meeting had been prepared and sent. Dr. Laura A. Kolk was elected to serve the unexpired (one-year) portion of Dr. Levine's term as Council Member. The following committees were appointed for the year 1949:

*Field Committee:* Vernon L. Frazee (Chairman), Louis E. Hand, Harold N. Moldenke, James Murphy, G. G. Nearing, Rutherford Platt, William Rissanen, Farida A. Wiley; *Program Committee:* Jennie L. S. Simpson (Chairman), Charles A. Berger, Harold H. Clum, Marion A. Johnson, Elva Lawton, Edwin B. Matzke, Harold W. Rickett, Donald P. Rogers; *Publications Exchange Committee:* Jennie L. S. Simpson (Chairman), Amy L. Hepburn, Harold W. Rickett.

Dr. James E. Gunkel of Rutgers University spoke on "Growth habit, shoot expression and the mechanism of its control in *Ginkgo biloba*." His abstract of the address follows:

Two well-defined types of shoots, namely *long shoots* and *short shoots*, occur in *Ginkgo*. A short shoot of any season may in any season assume the long-shoot habit. Conversely, a long shoot of one or more previous seasons may in any season fail to produce internodal growth and so assume the short-shoot habit.

The excurrent type of growth habit in young *Ginkgos* is due to the formation of terminal long shoots. The broadening of trees with age is due to changes in shoot expression, the mature trees having equal numbers of long- and short-shoot terminals. The older the plant or the older the buds the less chance for shoot reversal, unless disturbed by an injury.

Decapitation of young plants causes short-shoot laterals to develop into long shoots. Application of naphthaleneacetic acid to the cut surface maintains the laterals in the short-shoot condition, as in intact plants, suggesting terminal-bud inhibition for controls.

Approximate rules have been developed for determining in selected cases whether a bud will develop into a long or short shoot. The yield of diffusible auxin from short-shoot buds rises from zero in the "tight" stage to a maximum at first greening and then decreases as the buds open. Long shoots behave similarly, but after the auxin yield has fallen with bud opening it rises steeply with the beginning of elongation. Auxin production by the long shoot in its youngest leaves and internodes then becomes very small, while large amounts are produced by the lower, rapidly extending internodes. The diffusible auxin is in excess of that used in shoot elongation. The total yield per shoot increases with the number of nodes rather than with the length of the shoot. The auxin is not produced by the leaves or the apical meristem, but reasons exist for concluding that it is produced (or activated) in the stem itself, while the young leaves may supply an inactive auxin precursor.

Bud development is considered as taking place in two stages, i.e. (1) opening and leaf enlargement (2) axis elongation and associated growth so that lateral short shoots become a special case of bud inhibition in which only stage (2) is inhibited. However, growth data show that where auxin supply is adequate the ability of long shoots to develop from laterals is also some function of the general nutrition of the plant.

Acropetally developing procambial strands project into the region of presumptive leaf primordia before the primordia appear. This precocious development of the primary vascular system, together with the physiology of shoot growth, are offered as evidence that the pattern of shoot growth is not alone a property inherent in the stem apex, as some have suggested, but that the physiology and pattern of development of older stem tissues are, if not a controlling factor, at least a corollary to shoot growth.

The meeting was adjourned at 9:40. Refreshments were served by the Hunter staff.

**Minutes of the meeting of February 16, 1949.** The meeting was called to order at Hunter College by President Matzke at 8:10 P.M.; 37 members and friends were present. The minutes of the preceding meeting were read and approved; no other business was transacted. Mr. G. G. Nearing of Demarest, N. J., spoke on "Lichens we see on field trips," illustrating his discussion with color photographs.

The meeting was adjourned at 9:45; afterward refreshments were served by the Hunter College botanists.

Respectfully submitted  
DONALD P. ROGERS  
Recording Secretary.

**Minutes of the meeting of March 1, 1949.** The meeting was called to order at Columbia University by President Matzke at 8:10 P.M.; 22 members and friends were present. The minutes of the preceding meeting were read and approved. Dr. Francis J. Ryan of Columbia University spoke on "Adaptation of biochemical mutants of microorganisms." His abstract follows:

Microorganisms are renowned for their ability to adjust to unfavorable conditions in their environment. For example, a mutant of the mold *Neurospora crassa* which requires the amino acid leucine for growth may adjust to a low concentration of leucine by developing the ability to synthesize this substance. By the use of genetic techniques it has been possible to show that adaptations are the result of back-mutations of genes which cannot enable leucine synthesis to a condition where they can. Such mutations result in a heterogeneous mixture of nuclei within the mycelium and a competition is set up between the two types. The outcome of this competition depends upon environmental conditions which, then, through their selection for or

against mutant genes, will determine whether adaptation occurs. In the bacterium *Escherichia coli* back-mutations in growth-factor-requiring strains similarly return synthetic ability. The competition between back-mutant and parent leads to adaptation when a poor supply of growth factor is present. In the presence of an adequate supply of growth factor an equilibrium is reached so that a growth-factor-requiring culture is stable but always possessed of a few back-mutant growth factor-independent organisms. Thus even the "training" of microorganisms when examined closely turns out to be explained by mutation and selection.

The meeting was adjourned at 9:45 P.M.

Respectfully submitted

ANNETTE HERVEY

*Recording Secretary pro tem.*

### NOTE

Still another new botanical periodical of international scope has issued its first number. This is *Phyton*, or *Annales Rei Botanicae*, published in Horn, Austria, edited in Graz. The inserted announcement states that the purpose of *Phyton* is to cover the entire field of botany. Articles will be accepted in any of the languages of the International Botanical Congresses. The first issue contains articles on genetics, on taxonomy (including phytogeography), on plant physiology, on pollen analysis, and on several other topics. All but one are in German.

The magazine is well printed on good paper and attractively designed.

# INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

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WITH THE COLLABORATION OF THE EDITOR OF THE TAXONOMIC INDEX

## TAXONOMY, PHYLOGENY AND FLORISTICS

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## PHYTOTOXIC BLOOD SERA IN MEDICINE

DAVID I. MACHT

The present report is an admirable illustration of the advantages accruing both to pure research and to practical medicine from a collaboration between the various fundamental physical, chemical, and biological sciences with the basic medical sciences of physiology, pharmacology, and biochemistry.

Twenty-five years ago the present writer, who was at that time a lecturer in pharmacology at the Johns Hopkins Medical School and associated with the father of American pharmacologists, the famous Professor John J. Abel, conceived the idea of making a comparative study in regard to the action of drugs and chemicals between living plant protoplasm and living animal protoplasm. By pharmacology as it is taught in most of our medical schools is meant of course a study of the effects of drugs, chemicals, and poisons on living animal protoplasm, animal tissue, or whole animal organisms. In other words, it is strictly speaking *zoopharmacology*. However, just as there are two kinds of physiologies, namely, *zoophysiology* or animal physiology and *phytophysiology* or plant physiology, so the author thought to develop a new branch of biology to which he gave the name of *phytopharmacology* or the study of drugs and chemicals on living plant protoplasm, plant tissues, or whole plants (1, 2).

The effects of drugs and poisons on plants may be studied in many ways. The plant physiologist may study the effects of chemicals on the germination of seeds and respiration of seeds, on the growth of roots and stems and flowers, on the geotropic and heliotropic properties of plants, on the growth of yeasts and fungi, on the behavior of chloroblasts, on protoplasmic streaming, on the vital processes of photosynthesis, on oxidation and reduction phenomena, etc. In order to become familiar with plant physiological methods, the writer spent a year or more in the laboratories of the late Professor Burton E. Livingston of the Johns Hopkins University, who at that time was one of the leading plant physiologists in this country. In this way various methods of study were learned and selected as practicable for application to medical work.

The most practical and fruitful approach to phytopharmacological problems was found to be in pursuing quantitative phytopharmacological studies on the root growth of *Lupinus albus* seedlings under standardized conditions of light, temperature, humidity, and many other ecological factors. These methods have been described in full in various publications

by the writer and his collaborators. It was found very early by means of special phytopharmacological techniques that living plants responded often very differently to drugs and chemical agents from the way the same drugs or chemicals affected living animals. Thus for instance, by means of living plant test-objects one could easily distinguish between solutions of organic and inorganic mercury compounds. Again, by means of such very sensitive plant physiological test-objects, one could differentiate even between stereoisomers. Table 1 illustrates well how sensitive seedlings of *Lupinus*

TABLE 1. *Growth of Lupinus albus Seedlings in Solutions of Some Isomers.*

Drug or Chemical	Optic Variety	Concentration in Shive	Phytotoxic Index per cent
Quinine Sulfate	Levo-rotatory	1: 2000	67
Quinine Sulfate	Levo-rotatory	1: 4000	71
Quinidine Sulfate	Dextro-rotatory	1: 2000	90
Quinidine Sulfate	Dextro-rotatory	1: 4000	94
Cinchonidine Sulfate	Levo-rotatory	1: 1000	69
Cinchonine Sulfate	Dextro-rotatory	1: 1000	91
Leucine (alpha-amino-iso-butyl acetic acid)	Levo-rotatory	1: 100	81
Leucine (alpha-amino-iso-butyl acetic acid)	Racemic	1: 100	102
Camphor	Racemic	1: 10000	53
Camphor	Dextro-rotatory	1: 10000	62
Ortho-saligenin		1: 5000	27
Meta-saligenin		1: 5000	62
Para-saligenin		1: 5000	81
Brom-ortho-saligenin		1: 5000	22
Brom-meta-saligenin		1: 5000	41
Brom-para-saligenin		1: 5000	71

*albus* are to various chemical compounds dissolved in plant-physiological solution. Here we see also the difference in phytotoxicity produced by isomeric organic compounds. Not only is there a difference in toxicity exhibited by the two sets of *structural* isomeric compounds, the saligenins and brom-saligenins, the formulae of which are subjoined (fig. 1), but also by stereoisomers such as those of quinine, cinchonine, leucine, and camphor. Thus for instance, the stereoisomers of quinine, nicotine, adrenalin, and camphor exerted different degrees of inhibition on the root growth of *Lupinus albus* seedlings. The most striking finding, however, was the marked difference between drugs or chemicals derived from the animal world and drugs and chemicals derived from the plant world. Zoogenetic chemicals were found to be much more toxic for living plant protoplasm

than phytogetic substances. On the other hand, phytogetic drugs were in general much more poisonous for animal protoplasm than for plant protoplasm.

A single illustration will be very enlightening. Epinephrine or adrenalin is a drug derived from the superarenal glands of animals. It was found to be a very powerful zoopharmacological agent, as is generally known, but it is not generally known that when tested on living plant protoplasm epinephrine is even more toxic for the root growth of *Lupinus albus* seedlings. Vice versa, the drug known as ephedrine, sometimes called "vegetable adrenalin," which is substance derived from the plant world but possessing certain pharmacological properties similar to those of adrenalin

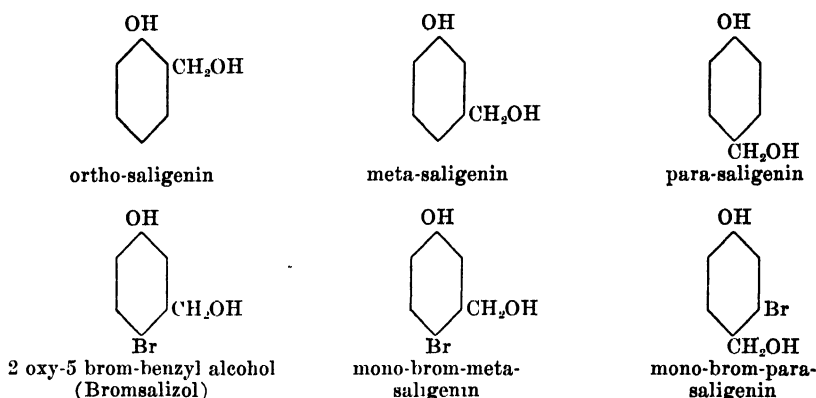


FIG. 1. Chemical structure of certain isomers.

for animals, was found to be much more toxic for animal tissues than for plant tissues.

The most important phytopharmacological findings made by the author and his associates, however, belong strictly to the medical field and are concerned with the biological properties of blood and blood serum. By employing his special technique the author was successful in demonstrating for the first time certain toxic substances in the blood of animals, including man, which could not heretofore be demonstrated either by zoopharmacological methods or even by ordinary chemical and physiological experiments.

Before describing briefly some of these findings with blood, we must define the term often employed by the writer, namely, index of growth. By the index of growth is meant the ratio of the root growth of a series of *Lupinus albus* seedlings grown in plant physiological hydroponic solutions to the growth of seedlings from exactly the same crop in exactly the same plant physiological solutions to which a small percentage (usually 1

per cent) of blood serum or other chemical or drug has been added. In other words,

$$\text{Index of growth} = \frac{X}{N} \times 100$$

It was found on examining the blood sera of all kinds of animals, both cold-blooded and warm-blooded, that the phytotoxic index of a 1 per cent solution usually ranges between 70 and 75 per cent. The only exception to this rule is the blood serum of reptiles (snakes, alligators, lizards, turtles, gila monsters, etc.) which was found to be more toxic than that of other animals. In fact, it was found that the blood serum of so-called non-venomous snakes, or snakes which possess no poison glands, was just as toxic as the blood serum of virulent poisonous reptiles.

On examining the blood of human beings, it was found that the blood sera of normal individuals, both male and female, as well as blood sera from infectious diseases of bacterial origin were found to be non-toxic. To this there were only a few exceptions and this fact made the exceptions very important. Among the toxic blood sera of human beings were found to be, first, the blood serum of women during menstruation; and the phytopharmacological technique yielded the first quantitative experimental demonstration of the presence of such a menstrual poison, or *menotoxin*, which was suspected even in the most remote antiquity (3).

The next condition in which the blood was found to be toxic was pernicious anemia, in both sexes of course (4). Here the blood serum of pernicious anemia patients yielded a very toxic index of growth in contrast to the sera of all other kinds of anemias and leukemias. This finding became useful in the differential diagnosis of doubtful cases of pernicious anemia, and furthermore, as described elsewhere, it showed that the so-called liver treatment of pernicious anemia, while improving the morphological blood picture of patients and their general condition, did not destroy the toxic substances present in their blood. However, exposure of their blood both in vitro and clinically to ultraviolet radiation did produce a complete detoxification of pernicious anemia toxin. Another condition in which a toxic substance was demonstrated in the blood of human beings by plant physiological methods is leprosy (5). Still another disease was trachoma (6). This grave eye disease which was originally regarded as a local inflammation of the conjunctiva was thus proven to be a systemic disease with local ocular manifestations.

In the present communication the author wishes to call attention to three other conditions on which he has been working for many years and which have yielded very useful information through phytopharmacological studies, which information became of practical therapeutic and clinical

value in medical practice. The first of these is the very fatal disease known as pemphigus, a study of which was begun by the author with his late classmate and friend, the dermatologist Dr. I. R. Pels. A routine examination by phytopharmacological methods of blood sera from all kinds of dermatoses revealed that in all of them with the exception of two, the blood sera yielded a phytotoxic index the same as that of normal sera. The two exceptions were, first, leprosy which was just mentioned, and, second, the very grave disease with ninety per cent mortality known as pemphigus (7). Pemphigus is generally regarded as a skin disease but the recent studies by the present writer and his collaborators have definitely established that it is no more of a skin disease than smallpox. In other words, it is a systemic illness giving a characteristic toxic reaction of the blood and affect-

TABLE 2. *Comparison of Blood Sera.*

	Phytotoxic Index	Serum	Phytotoxic Index
	per cent		per cent
1. Normal human serum	70-75	13. Mononucleosis	80
2. Menstrual	51-60	14. Bacterial Infections	70-75
3. Pernicious Anemia	44-57	15. Eclampsia	75
4. Pemphigus	48-60	16. Syphilis	81
5. Leprosy	47	17. Tuberculosis	78
6. Trachoma	48	18. Scarlet Fever	79
7. Severe Secondary Anemia	65-69	19. Measles	80
8. Carcinoma	70	20. German Measles	80
9. Malarial	70	21. Varicella	80
10. Banti's Disease	75	22. Post Puerperal (12 wks)	80
11. Lymphatic Leukemia	70	23. Vaccinia virus	80
12. Myelogenous Leukemia	70	24. Herpes Simplex	84

ing the patient's constitution very profoundly, and is accompanied by characteristic bullae and other skin lesions. So striking is the phytopharmacological action of pemphigus serum that the so-called Macht-Pels reaction or test is now generally accepted as a valuable diagnostic criterion for this disease, and specimens for diagnosis are received in the author's laboratory almost every week. A further advance in the knowledge of this disease was made more recently by the writer in association with the late radiologist, Dr. Marcus Ostro of the Sinai Hospital, Baltimore, when they discovered that when pemphigus serum *in vitro* is irradiated with especially filtered hard X-rays for a few minutes the toxicity of the serum is destroyed (8). This finding *in vitro* was the starting point of a new therapeutic procedure in treating some patients afflicted with this hopeless disease, and it was found that cautious irradiation of these patients with deep X-rays in small doses over the spleen and liver produced a detoxification of their blood which was followed by more or less clinical improve-

ment in their general condition and skin lesions. In this way at least half-a-dozen patients have been saved from almost certain death by these phytopharmacological discoveries. In table 3 is given a protocol of a remarkable case of pemphigus, that of Mrs. J. B. who was in a moribund condition. and who was saved by treatment with small doses of deep X-rays, filtered through a composite filter of 2 mm. copper and 1 mm. of aluminum. Such cases are described in detail by Macht and Ostro in a medical journal.

A second important condition in which phytopharmacology has led to

TABLE 3. *Effect of Radiotherapy on a Case of Pemphigus, showing change in Phytotoxicity.*

PROTOCOL B. Pemphigus Case Mrs. B.			
Date	Phytotoxic Index	Date	Phytotoxic Index
Dec. 4, 1945 In very bad shape, moribund	50%	Mar. 4	90%
Dec. 6 Radiated ant. spleen 105r comp. filter 2 Cu		Mar. 18	72%
Dec. 7	61%	Mar. 25 Radiated liver 42r	
Dec. 8 Radiated ant. spleen 105r		Mar. 27	83%
Dec. 9	75%	April 4 Definite improvement	70%
Dec. 10 Radiated liver 110r		April 11 Definite improvement	71%
Dec. 13	78%	April 15 Discharged in greatly im- proved condition	72%
Dec. 19	88%	May 23 Well	69%
Dec. 27	89%	June 13 Well	68%
Discharged improved, no lesions.		July 15 Well	70%
Jan. 8, 1946 Few blebs reappear- ing	62%	Aug. 21 Well	80%
Feb. 13 Readmitted, relapse	50%	Sept. 23 Well	70%
Feb. 18 Radiated ant. spleen 63r		Nov. 6 Well	71%
Feb. 20 Radiated ant. spleen 63r	75%	Mar. 13, 1947	71%
Feb. 22 Radiated liver 63r		May 15 Quite well	72%
Feb. 26	90%	June 9 Quite well	72%
		Oct. 10 Quite well	72%
		Mar. 1, 1948 Quite well	72%
		Dec. 23 Entirely well	72%
		Mar. 1, 1949 Quite well	72%

interesting discoveries which promise to become of clinical value are studies on the pharmacology of the blood sera from all kinds of mental patients which the present writer has been carrying on for the last ten years with the aid of physicians from various state hospitals for the insane. It was discovered by him that all psychoses, whether the so-called organic psychoses or the so-called functional psychoses, yield toxic reactions when examined by his special phytopharmacological methods. Thus toxic reactions were produced by blood sera from manic-depressive patients, schizophrenics, involutional melancholia, paresis, and other insanities. In contrast to these, ordinary neurological, neurasthenic, and psychoneurotic patients yielded blood sera which behave exactly like normal human serum. The importance of these findings will be stressed by the writer in a more

detailed communication to be presented in the near future before special medical societies, but it is obvious that these findings promise to become a valuable aid both in differential diagnosis of true insanities and also as a starting point of criterion for evaluating therapeutic procedures. In table 4 are given the phytotoxic readings obtained by the writer with the blood sera of some psychotic patients. Such studies, owing to their obvious importance, have been in progress for a number of years, and will be presented in detail in the near future.

In the last three years the author has been interested in another very baffling though not fatal disease, namely, psoriasis. This is a very troublesome and disagreeable skin affliction concerning which very little is known and the writer has been fruitlessly seeking for an approach to the pathology of this disease. Recently, a new approach was devised and promises

TABLE 4. *Phytotoxic Indices of Some Psychotic Blood Sera.*

Patient	Diagnosis	Phytotoxic Index per cent
E. S.	Schizophrenia, catatonic hypokinetic type	44
H. R.	Schizophrenia, catatonic hypokinetic type	42
F. N.	Schizophrenia, catatonic hyperkinetic type	58
D. H.	Schizophrenia, catatonic hyperkinetic type	58
C. H.	Involuntional melancholia type	52
M. R.	Involuntional melancholia type	50
B. B.	Manic-depressive type	54
J. H.	Manic-depressive type	57

to be of considerable value both in diagnosing psoriasis and as a criterion in evaluating various treatments employed by physicians for this condition. The approach was through *phytopathological* lines. All of the phytopharmacological studies on blood were hitherto carried on by him by employing normal and healthy *Lupinus albus* seedlings. Now, it is well known that various plant physiologists and especially those in Russia have reported a remarkable success in agricultural and horticultural experiments by the employment of so-called "yarovized" plants. This phenomenon of "yarovization" is perhaps better known among English-speaking physiologists as "vernalization." A simple method of producing yarovized seedlings is by exposure of such seedlings for a period of twenty-four hours to low temperatures, but not temperatures low enough to kill the plants. By employing such vernalized seedlings the author recently demonstrated a marked difference in the phytotoxic indices given by solutions of the well-known drug ethyl-carbamate or *urethane* which is now being studied by medical investigators in connection with leukemia and cancerous growths. It was found that whereas even quite concentrated solutions of urethane



inhibit the root growth of ordinary *normal* lupine seedlings but very little indeed, a markedly phytotoxic action was exerted by very much more dilute concentrations of the same drug on vernalized seedlings. Employing the same technique in studying the blood sera of psoriasis, the author succeeded in demonstrating a definite phytotoxic effect produced by psoriasis serum on vernalized plants although normal plants were not affected by such sera at all and in fact gave higher indices even than normal blood sera. In this way already a series of psoriatic cases were studied and in

TABLE 5. *Psoriasis Sera Versus Control Sera.*

Psoriasis Sera				Control Sera			
Normal Plants	Phyto-toxic Index	Verna-lized Plants	Phyto-toxic Index	Normals Plants	Phyto-toxic Index	Verna-lized Plants	Phyto-toxic Index
No.	per cent		per cent		per cent		per cent
1	83		65	Normal human serum	75		75
2	70		49	" " "	77		70
3	82		51	" " "	71		71
4	82		43	" " "	71		75
5	88		43	" " "	72		75
6	81		50	" " "	78		78
7	91		56	Cat blood serum	84		84
8	70		50	" " "	71		74
9	81		49	Carcinoma	74		75
10	99		58	B. 875	70		73
11	91		64	B. 876	71		73
12	77		53	B. 880	70		73
13	86		53	B. 883	66		69
14	81		41	Scleroderma	87		86
15	90		49	Leukemia (lymph)	78		76
16	82		57	Schizophrenia	42		48
17	76		58	Manic depressive	33		35
18	85		63	Lupus erythematosus	65		63
19	93		52	Menstrual serum	55		52
20	86		62	Pernicious anemia	55		52
21	82		45	" "	53		53
22	70		52	Pemphigus	44		44
23	73		47	" "	51		53
24	92		37	" "	58		54
Av. Index 82.9		Av. Index 50.7					

each case a phytotoxic effect on yarovized plants was demonstrated. Control experiments with normal blood-sera and sera from various other diseases revealed that they do not affect significantly or at all such yarovized plants. This new psoriasis test promises to be useful in evaluating the results of different methods of therapy. For instance, the author has found in vitro that psoriatic blood serum exposed to ultraviolet rays is no longer toxic for vernalized plants and it is well known that ultraviolet irradiations are employed by dermatologists in psoriatic patients. The same was

found in vitro after exposure of psoriasis sera to small doses of filtered X-rays. Finally, a detoxification was produced in vitro of psoriatic blood serum which was mixed with small doses of *sarsaponin*, an active principle found in the plant root of *Smilax sarsaparilla*<sup>1</sup>. Studies as to whether patients treated with various agents such as just mentioned and with other agents will yield a detoxified psoriatic blood are now in progress. It is thus seen that the opening of a new experimental approach to studying biological phenomena, namely, with the development of the new branch of biology to which the name *phytopharmacology* has been given, discoveries have been made which are both of purely scientific interest and at the same time of considerable value in studies on the diagnosis, pathology, and therapy of different clinical conditions in men.

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<sup>1</sup> Furnished by the courtesy of Ernst Bischoff Co., Inc., Ivoryton, Connecticut, under the name of "Sas-Par."

## ANTIBACTERIAL ACTIVITY OF SEEDLING EXTRACTS OF CULTIVATED PLANTS

HUBERT A. HARRIS

Since the first extensive survey of higher plants for antibacterial substances by Osborn (1943), similar surveys have been conducted by Huddleson, DuFrain, Barrons, and Geifel (1944), Lucas and Lewis (1944), Sanders, Weatherwax, and McClung (1945), Carlson, Bissell, and Mueller (1946), Hayes (1947), and Carlson, Douglas, and Robertson (1948).

Among these surveys are included some cultivated plants, but chiefly they involved tests on field collections of wild plants. Cultivated plants, containing antibacterial substances of therapeutic value, would, in general, have greater economic production advantages over wild plants possessing such substances because of their greater adaptability to commercial propagation.

Screening tests of higher plants for antibacterial substances have presented investigators with several difficulties. Aside from the task of collecting widely scattered plants in the field and maintaining them in a fresh condition for testing, the antibacterial substances are not always of general occurrence in the plant. Instead, it has been reported that they may be concentrated only in a single part such as the root, stem, bark, leaf, flower, fruit, or seed. Tests are therefore necessitated on each separate plant part and certain parts frequently are unavailable from field specimens. Antibacterial activity, too, has been determined to be influenced by varietal character, age of the plant, and the temperature under which the plant is growing when collected. More recently, and during the course of the present investigation, Carlson and Douglas (1948) have shown that screening tests of plants for antibacterial substances require the use of more than one solvent for extractives before a plant can be discarded as lacking antibacterial activity.

Irving, Fontaine, and Doolittle (1945) reported that lycopersicin, later renamed tomatin by them (1946), was absent in the seed of the tomato plant, but appeared in seedlings germinated in the dark and in the plant within eight days after planting. Screening tests could be partially simplified if seedlings contain antibacterial substances that persist in the mature plant. It is recognized that such substances in the mature plant may not be present in the seedling stage, but, conversely, antibacterial substances may possibly be transitory in seedlings and not occur in mature plants. This presents no serious objection, however, since one of the

chief objectives of screening tests is to discover indications of antibacterial activity for further investigation. Screening tests do not purport altogether to exhaust the antibacterial possibilities of extracts of individual plants; hence positive antibacterial activity in seedling extracts might afford valuable data.

TABLE I. *Antibacterial Activity of Seedling Extracts.*

Seedling	E. col.	S. mar.	S. lut.	S. aur.
Compositae				
<i>Carthamus tinctorius</i> (saffron) 661	-	++	-	-
<i>Cynara cardunculus</i> (cardoon) 661	-	+++P	+++	+
<i>Cynara scolymus</i> (artichoke) green globe 3	-	++P	+++	+
Convolvulaceae				
<i>Ipomea noctiflora</i> (moon flower) 376	-	-	++	-
Cruciferae				
<i>Brassica oleracea</i> var. <i>italica</i> (sprouting broccoli) Italian green sprouting 159	-	-	+	-
<i>Cheiranthus cheiri</i> (wallflower) 382	++P	+++P	+	-
<i>Iberis umbellata</i> (candytuft) 208	-	+++P	+++	-
* <i>Iberis umbellata</i> (candytuft) 208	-	+P	++	-
<i>Malcomia maritima</i> (Virginian stock) 381	++P	++P	+++	+
* <i>Malcomia maritima</i> (Virginian stock) 381	++P	+++P	++	+
Gramineae				
<i>Zea mays</i> var. <i>saccharata</i> (sweet corn) golden bantam extra early 851	-	-	++	-
Liliaceae				
<i>Allium cepa</i> (onion) yellow globe Danvers 77	-	-	-	+
<i>Allium porrum</i> (leek) large American flag 171	-	-	++	-
Rosaceae				
<i>Geum chilense</i> (Mrs. Bradshaw geum) 344	+	+	-	-
Solanaceae				
<i>Capsicum frutescens</i> var. <i>grossum</i> (bell pepper) ruby king 97	-	-	+	-
<i>Lycopersicum esculentum</i> (tomato) ponderosa 133	-	-	+	-
Tropaeolaceae				
<i>Tropaeolum peregrinum</i> (canary bird vine) 302	-	++P	++P	-

\* Antibacterial activity of mature plant extract.

- = no inhibition.

+ = 13-16 mm. zone of inhibition.

++ = 17-21 mm. zone of inhibition.

+++ = 22-26 mm. zone of inhibition.

++++ = 27-30 mm. zone of inhibition.

P = partial inhibition.

The results of a preliminary test indicated sufficient correlation between comparative tests on the occurrence of antibacterial substances in the extracts of 15 different species of seedlings and the extracts of the mature stages of these same plants to warrant a more extensive survey for antibacterial substances in cultivated plants using seedling extracts.

In this preliminary test, seedling extracts of two species of plants belonging to the Cruciferae, *Iberis umbellata* (candytuft) and *Malcomia maritima* (Virginian stock), showed comparable antibacterial activity for both the seedling extracts and the mature plant extracts as shown in table 1. The extracts of both seedlings and mature plants of 13 different species of plants showed negative antibacterial activity with all four bacterial test organisms. These plants were as follows: Convolvulaceae, *Quamoclit pinnata* (cypress vine), *Q. sloteri* (cardinal climber); Caryophyllaceae, *Dianthus chinensis* var. *heddewigii* (pinks); Labiatae, *Satureia hortensis* (summer savory); Leguminosae, *Pisum sativum* (garden pea); Linaceae, *Linum grandiflorum* var. *rubrum* (scarlet flax); Malvaceae, *Althaea rosea* (hollyhock); Nyctaginaceae, *Mirabilis jalapa* (four o'clock); Papavaraceae, *Escholtzia californica* (california poppy); Scrophulariaceae, *Delphinium hybridum* (larkspur); Solanaceae, *Petunia hybrida* (common garden petunia), *Nicotiana alata* var. *grandiflora* (flowering tobacco); Tropaeolaceae, *Tropaeolum majus* (garden nasturtium).

The present investigation reports in vitro tests for water-soluble antibacterial substances in 145 different species and varieties of cultivated plant seedlings belonging to 37 different families, using two Gram-negative and two Gram-positive bacteria as test organisms.

**Materials and Methods.** The various seeds<sup>1</sup> were planted in moist sand in greenhouse flats and the seedlings, except in a few instances of slow germination, were two to three weeks old when tested for antibacterial properties. Greenhouse temperatures were 20–30° C. The seedlings were freed of sand by several rinsings in distilled water and the entire seedlings were crushed thoroughly with mortar and pestle to extract the juice, which was tested immediately against each of the following four bacteria: *Escherichia coli*: ATCC 9739. *Serratia marcescens*: ATCC 4261. *Staphylococcus aureus*: Oxford strain H, ATCC 9144. *Sarcina lutea*: stock laboratory culture, source unknown.

The filter paper disc method of Vincent and Vincent (1944) was used to determine comparative qualitative tests of antibacterial substances in the seedling extracts. Filter paper discs (Schleicher and Schuell, no. 740-E, 12.7 mm. diam.) were saturated in the test extract, the excess fluid gently shaken off, and placed on seeded nutrient agar plates. Six discs, comprising duplicate tests of extracts from three different kinds of seedlings, were spaced equidistant on each agar plate.

Before being used for seeding the agar plates, each bacterial test organism was transferred three times on successive days to 10 ml. of nutrient broth. All broth cultures, save those of *S. marcescens*, were incubated at

<sup>1</sup> The seeds used in these experiments were supplied by the courtesy of the Northrup and King Seed Company, Minneapolis, Minnesota.

37° C for 16–20 hrs. The latter cultures were incubated at room temperature (23–27° C).

Nutrient agar was dispensed (20 ml.) into sterile petri dishes with a sterile pipette; the surface of the solidified agar was flooded with a culture suspension of the test organism and the excess suspension pipetted off. The surfaces of the flooded agar plates, with the covers removed, were dried for 45 min. in a 37° C incubator. The test plates were incubated at the same temperatures and for the same time intervals as for the test bacteria in nutrient broth.

Measurements were recorded to the nearest 0.5 mm. of the outside diameters of the inhibitory zones of the test organisms by means of pointed dividers under a magnifying lens.

**Experimental Results.** Many of the varieties of cultivated plants used in this investigation are either unknown or doubtful even to the seedsmen. Consequently, the varieties tested are listed only for certain ones, but all plants tested are more specifically referred to by the seed company's packet number which is listed after each plant name. The nomenclature employed, with few exceptions, is that of Bailey (1927).

As shown in table 1, positive tests for antibacterial activity, against one or more test organisms, were obtained with seedling extracts of 17 different species of cultivated plants belonging to nine different families,

The antibacterial substances, in general, were more effective against the Gram-positive than Gram-negative bacteria. With few exceptions, the latter organisms were only partially inhibited or not at all. The seedling extract of only one plant species, *Malcomia maritima* (Virginian stock), showed some activity against all four test organisms.

Seedling extracts of the following plant species or varieties exhibited negative antibacterial activity with all four test organisms.

**Amaranthaceae**

*Celosia argentea* (plumed cockscomb) 340

*Gomphrena globosa* (globe amaranth) 398

**Apocynaceae**

*Vinca rosea* (Madagascar periwinkle) 380

**Balsaminaceae**

*Impatiens balsamina* (garden balsam) 202

**Boraginaceae**

*Anchusa capensis* (bluebird) 226

*Borago officinalis* (borage) 3379

*Cynoglossum amabile* (cynoglossum) 212

*Myosotis sylvatica* (forget-me-not) 364

**Campanulaceae**

*Campanula medium* var. *calycanthema* (cup and saucer Canterbury bell) 338

*Lobelia erinus* var. *compacta* (lobelia) 345

**Capparidaceae**

*Dianthus barbatus* (sweet William) 4851

*Dianthus caryophyllus* (carnation) 333

- Dianthus chinensis* var. *heddewigii* (pinks) 216  
*Gypsophila elegans* (baby's breath, crimson) 264  
*Gypsophila elegans* (baby's breath, white) 214

## Chenopodiaceae

- Beta vulgaris* (beet) Detroit dark red turnip 3  
*Beta vulgaris* var. *cicla* (Swiss chard) Fordhook giant 8  
*Beta vulgaris* var. *crassa* (sugar beet) U. S. strain 199  
*Kochia trichophylla* (summer cypress) 215  
*Spinacia oleracea* (spinach) Bloomsdale 118

## Compositae

- Ageratum houstonianum* (floss flower) 359  
*Artemisia absinthium* (wormwood) 661  
*Bellis perennis* (English daisy) 358  
*Brachycome iberidifolia* (Swan river daisy) 337  
*Calendula officinalis* (pot marigold) 204  
*Callistephus chinensis* (China aster) 301  
*Centaurea cyanus* (bachelor's button) 203  
*Chrysanthemum maximum* (Shasta daisy) 353  
*Cichorium endiva* (endive) green curled 166  
*Cichorium intybus* (chicory) witloof 163  
*Coreopsis coronata* (tickseed) 276  
*Coreopsis lanceolata* (coreopsis) 271  
*Cosmos bipinnatus* (cosmos) 210  
*Dahlia pinnata* (dahlia) 387  
*Gaillardia aristata* (gaillardia) 375  
*Helianthus annuus* (sunflower) 232  
*Lactuca sativa* (lettuce) black-seeded Simpson 46  
*Lactuca sativa* var. *romana* (cos lettuce) Paris white cos 184  
*Tagetes erecta* (African marigold) 346  
*Taraxacum officinale* (common dandelion) improved thick leaf 177  
*Thelesperma hybridum* (cosmidium) 257  
*Tragopogon porrifolius* (salsify) Sandwich Island 115  
*Zinnia grandiflora* (zinnia) 289

## Convolvulaceae

- Ipomoea noctiflora* (moonflower) 376  
*Quamoclit pinnata* (cypress vine) 305  
*Quamoclit sloteri* (cardinal climber) 339

## Cruciferae

- Alyssum maritimum* (sweet alyssum) 223  
*Brassica caulorapa* (kohl-rabi) early white Vienna 169  
*Brassica juncea* (Chinese mustard) Chinese broad leaf 173  
*Brassica napobrassica* (rutabaga) American purple top 151  
*Brassica oleracea* var. *acephala* (collards) Georgia 164  
*Brassica oleracea* var. *acephala* (kale) dwarf green curled 168  
*Brassica oleracea* var. *botrytis* (cauliflower) snowball No. 16 domestic 30  
*Brassica oleracea* var. *capitata* (cabbage) late flat Dutch 16  
*Brassica oleracea* var. *gemmifera* (Brussel's sprouts) Long Island improved 179  
*Brassica pekinensis* (Chinese cabbage) Chihili 195  
*Brassica rapa* (turnip) purple top strap leaved 145  
*Eruca sativa* (rocket) 661  
*Lepidium sativum* (garden cress) curled 86  
*Raphanus sativus* (radish) early scarlet turnip 106

## Cucurbitaceae

- Citrullus vulgaris* (watermelon) Kleckley's sweets 64  
*Cucumis melo* var. *reticulatus* (muskmelon) Rocky Ford 55  
*Cucurbita pepo* (field pumpkin) early sweet sugar 101

- Cucurbita pepo* var. *condensa* (summer squash) giant summer crook neck 121  
*Cucurbita pepo* var. *ovifera* (ornamental gourd) 365  
*Cucumis sativus* (cucumber) Boston pickling 37
- Dipsacaceae
- Scabiosa atropurpurea* (mourning bride) 236
- Euphorbiaceae
- Euphorbia marginata* (snow on the mountain) 270  
*Ricinus communis* (castor bean) 250
- Hydrophyllaceae
- Nemophila menziesii* var. *insignis* (baby blue eyes) 277
- Labiatae
- Hyssopus officinalis* (hyssop) 661  
*Melissa officinalis* (lemon balm) 199  
*Nepeta cataria* (catnip) 123  
*Ocimum basilicum* (basil) 51  
*Origanum majorana* (sweet marjoram) 156  
*Rosmarinus officinalis* (rosemary) 3376  
*Salvia officinalis* (sage) 157  
*Satureia hortensis* (summer savory) 193  
*Thymus vulgaris* (thyme) 158
- Leguminosae
- Dolichos lablab* (hyacinth bean) 265  
*Lathyrus odoratus* (sweet pea) 329  
*Lupinus hartwegii* (lupine) 266  
*Phaseolus vulgaris* var. *humilis* (bush bean) giant stringless green pod 809  
*Pisum sativum* (garden pea) little gem 835
- Liliaceae
- Asparagus officinalis* (garden asparagus) Mary Washington 50
- Linaceae
- Linum grandiflorum* var. *rubrum* (scarlet flax) 274
- Malvaceae
- Althaea rosea* (hollyhock) 307  
*Hibiscus esculentus* (okra) mammoth long green podded 174  
*Hibiscus sp.* (hibiscus) 219
- Nyctaginaceae
- Mirabilis jalapa* (four o'clock) 213
- Onagraceae
- Clarkia elegans* (clarkia) 363  
*Godetia grandiflora* (godetia) 272
- Papavaraceae
- Eschscholtzia californica* (California poppy) 205  
*Papaver rhoeas* (Shirley poppy) 234
- Polemoniaceae
- Phlox drummondii* (phlox) 378
- Portulacaceae
- Portulaca grandiflora* (rose moss) 348
- Polygonaceae
- Rheum rhaponticum* (garden rhubarb) mammoth Victoria 176  
*Rumex acetosa* (sorrell) 3374
- Ranunculaceae
- Aquilegia longissima* (long spurred columbine) 341  
*Delphinium hybridum* (larkspur) 217  
*Nigella damascena* (love in the mist) 273
- Resedaceae
- Reseda odorata* (common mignonette) 222



## Rutaceae

*Ruta graveolens* (rue) 661

## Scrophulariaceae

*Antirrhinum majus* (common snapdragon) 354

*Digitalis purpurea* (foxglove) 343

*Linaria maroccana* (linaria) 389

*Nemesia strumosa* (nemesia) 350

## Solanaceae

*Nicotiana glauca* var. *glauca* (flowering tobacco) 377

*Petunia hybrida* (common garden petunia) 243

*Salpiglossis sinuata* (painted tongue) 319

*Schizanthus wisetonensis* (butterfly bush) 237

*Solanum melongena* var. *esculentum* (eggplant) black beauty 165

## Tropaeolaceae

*Tropaeolum majus* (garden nasturtium) 225

## Umbelliferae

*Anethum graveolens* (dill) 155

*Apium graveolens* (celery) golden self-blanching 31

*Apium graveolens* var. *rapaceum* (celeriac) giant Prague 35

*Carum carvi* (caraway) 661

*Coriandrum sativum* (coriander) 2101

*Daucus carota* (carrot) Chantenay 28

*Ferula communis* (giant fennel) finocchio 2507

*Foeniculum dulce* (sweet fennel) 661

*Pastinaca sativa* (parsnip) improved hollow crown 92

*Petroselinum hortense* (parsley) dark moss curled 88

*Pimpinella anisum* (anise) 3380

*Trachymene caerulea* (blue lace flower) 336

## Verbenaceae

*Verbena hybrida* (common garden verbena) 249

## Violaceae

*Viola cornuta* (bedding pansy) 311

*Correlation of Results With Other Investigations.* Seven of the 15 plant species whose seedling extracts showed antibacterial action in the present investigation have been tested for antibacterial activity by other investigators. These seven are: *Brassica oleracea* var. *italica* (sprouting broccoli), *Cheiranthus cheiri* (wallflower), *Malcomia maritima* (Virginian stock), *Zea mays* var. *saccharata* (sweet corn), *Allium cepa* (onion), *Capsicum frutescens* var. *grossum* (bell pepper), and *Lycopersicum esculentum* (tomato).

Osborn (1943) found that the extracts of the seeds of white and purple varieties of sprouting broccoli inhibited *E. coli* and *S. aureus*.

She reported also that the vegetative extracts of the wallflower inhibited these same organisms as a result of enzyme action. Sanders (1946) reported that cheirolin, a substance extracted from the seeds of the wallflower, yielded negative effects on certain pathogenic fungi.

The extracts of the seeds of Virginian stock were reported by Osborn (1943) to inhibit *E. coli* and *S. aureus*.

The juice of sweet corn was reported by Little and Grubaugh (1946) to be inhibitive to *Eberthella typhosa*, *E. coli*, *Salmonella paratyphi* A,

*S. aureus*, *Erwinia carotovora*, *Phytomonas stewartii*, and two forms of the fungus *Fusarium oxysporum*, f. *melonis* and f. *niveum*.

The antibacterial properties of the onion, especially onion vapors, have been well established by Brown (1917), Sarti (1919), Walker, Lindegren, and Bachman (1925), Lovell (1937), Vollroth, Walton, and Lindegren (1937), Ingersoll, Vollroth, Scott, and Lindegren (1938), Fuller and Higgins (1940), Tokin (1943), Huddleson, DuFrain, Barrons, and Giefel (1944), Kovalenok (1944), Pederson and Fisher (1944), Toroptsev and Filatova (1944), Carpenter (1945), and Sanders, Weatherwax, and McClung (1945).

Seedling extracts of pepper were reported by Tokin (1943) to exhibit powerful bactericidal properties and to affect protozoa after prolonged exposure.

Irving, Fontaine, and Doolittle (1945) reported the extraction of an antibacterial substance, later termed tomatin (1946), from the tomato plant. This substance has become the subject of further investigations in a series of papers: Fontaine, Irving, and Doolittle (1947), Irving (1947), Fontaine, Ma, Poole, Porter, and Naghski (1947), Ma and Fontaine (1948), and Fontaine, Irving, Ma, Poole, and Doolittle (1948). Extracts of tomato plants were found by Little and Grubaugh (1946) to inhibit *S. paratyphi* A, *S. aureus*, and three forms of *Fusarium oxysporum*: f. *conglutinans*, f. *lycopersici*, and f. *melonis*. Pederson and Fisher (1944) and Carpenter (1945) reported little, if any, inhibition by tomato juice of certain bacteria.

Several of the species of plants whose seedling extracts yielded antibacterial activity in the present investigation have been tested for antibacterial properties by a number of other investigators.

Sherman and Hodge (1936) found juices of cabbage and turnip to inhibit *Aerobacter aerogenes*, *E. coli*, *Phytomonas campestris*, and natural mixed bacterial flora from the exterior of plant tissues. Negative antibacterial activity resulted with the juices of carrot, cucumber, and parsnip on the same bacteria.

Osborn (1943) found that the extracts of the seeds of Brussels sprouts, borecole, broccoli, cabbage, cauliflower, and kohlrabi inhibited *E. coli* and *S. aureus*, but extracts of the vegetative parts of these same plants produced only a slight partial inhibition of *S. aureus*.

Huddleson, DuFrain, Barrons, and Geifel (1944) reported that the juice of rhubarb inhibited *Brucella abortus* and *S. aureus*. The active substance was present only in the petiole of the plant.

Lucas and Lewis (1944) were unable to demonstrate antibacterial action of cabbage and turnip extracts against *E. coli*, *Phytomonas campestris*, *P. phaseoli*, and *S. aureus*.

Pederson and Fisher (1944) demonstrated the antibacterial activity

of cabbage juice toward certain Gram-negative bacteria occurring on the surface of cabbage leaves, *E. coli*, and *S. aureus*. Little, if any, inhibition was noted with juices of broccoli, Chinese cabbage, carrot, cauliflower, celery, cucumber, and turnip on the same bacteria.

Carpenter (1945) obtained negative antibacterial results with the juices of beet and celery on *E. coli*, *Pseudomonas aeruginosa*, and *S. aureus*.

Sanders, Weatherwax, and McClung (1945) found the extract of chicory to inhibit *E. coli* and *S. aureus*. The extracts of asparagus and the wild carrot failed to inhibit either organism.

Little and Grubaugh (1946) obtained inhibition of *E. typhosa*, and *S. paratyphi* A with bean juice. The juice of cauliflower inhibited *E. typhosa* and cucumber juice inhibited *Erwinia carotovora*.

Hayes (1947) found little or no inhibition of *E. carotovora*, *E. coli*, *Phytomonas tumefaciens*, and *S. aureus* with the extracts of asparagus, carrot, chicory, and dandelion.

Carlson, Douglas, and Robertson (1948) obtained negative antibacterial activity using aqueous extracts of mature sunflower plants against *E. coli* and *S. aureus*. However, ether extracts of the flowers completely inhibited *S. aureus*, but this organism was only partially inhibited by similar extracts prepared from the root-stem and leaf.

**Discussion.** The present investigation shows that seedling extracts are of value for antibacterial screening tests of higher plants and that such seedling extracts can be tested quite readily. The use of several extractive solvents, as recommended by Carlson and Douglas (1948), would be applicable with seedling extracts if the filter paper disc method of testing is employed since this method requires the use of very small quantities of test extracts.

The occurrence of antibacterial substances in seedling extracts compares favorably on a percentage basis with the screening tests of some other investigators employing the use of extracts from mature plants or plant parts. The results of some of these latter surveys show approximately the following percentages of plants possessing antibacterial properties to the total number of plants tested: Atkinson and Rainsford (1946), 15 per cent; Hayes (1947), 16 per cent; Sanders, Weatherwax, and McClung (1945), 10 per cent; Carlson, Bissell, and Mueller (1946), 4 per cent; and Carlson, Douglas, and Robertson (1948), 20 per cent. The results of the present investigation show 12 per cent.

The in vitro tests of the seedling extracts of cultivated plants indicate the presence of a few hitherto unreported antibacterial substances apparently worthy of further investigation.

## SUMMARY

1. Data are presented for *in vitro* screening tests for antibacterial substances in the seedling extracts of cultivated plants belonging to 37 different families using *Escherichia coli*, *Serratia marcescens*, *Sarcina lutea*, and *Staphylococcus aureus* for test organisms.

2. The use of seedling extracts is of value in screening tests of higher plants for antibacterial substances.

3. Approximately 12 per cent of the total number of different kinds of plant seedling extracts tested evidenced antibacterial properties.

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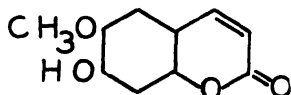
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## THE ISOLATION OF SCOPOLETIN, A BLUE-FLUORESCING COMPOUND FROM OAT ROOTS

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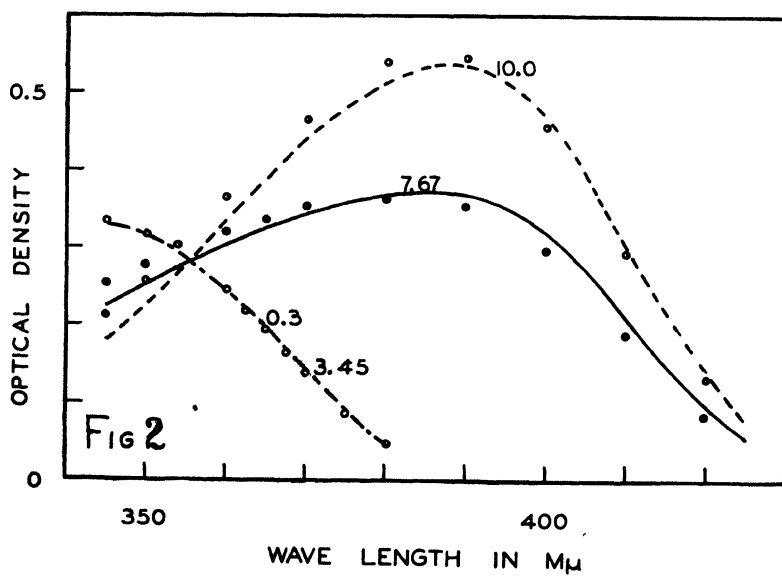
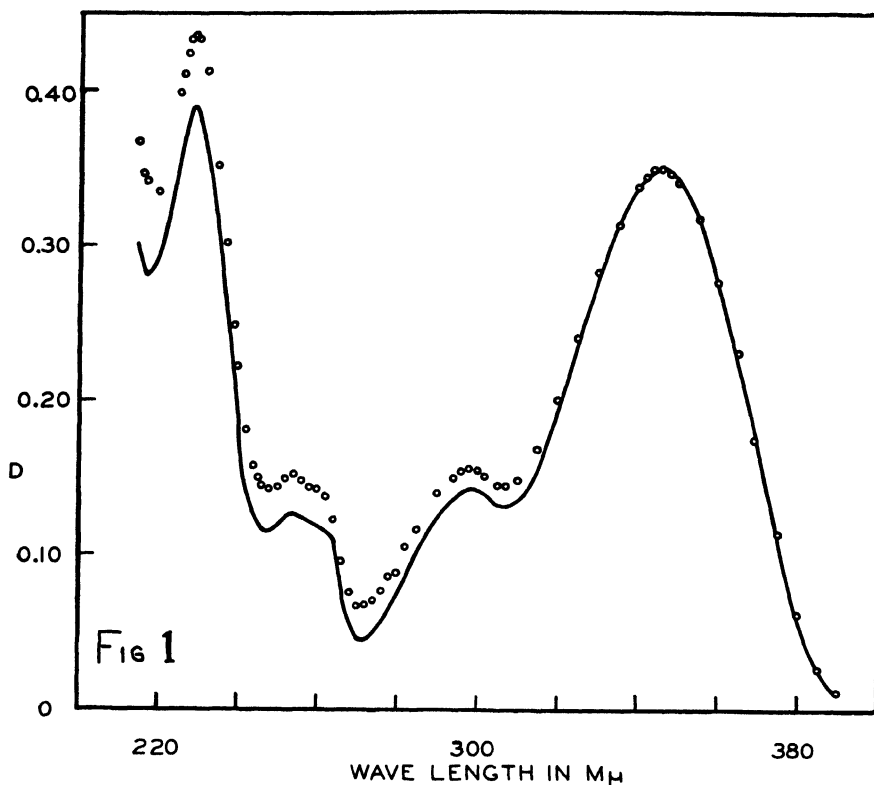
In an investigation of the fluorescence of roots (Goodwin & Kavanagh 1948), it was found that oats were a very rich source of a blue-fluorescing material, which was readily extracted with n-butanol, acetone, and other solvents. The extracts were separated into a number of different fractions, each of which exhibited different chemical properties. The fractions were distinguished by the relation between fluorescence and hydrogen ion concentration of the solution. The shapes of the pH-fluorescence curves were very distinctive.

The pH-fluorescence curves of a number of naturally-occurring organic compounds have been determined (Kavanagh & Goodwin 1949; and unpublished). Attempts to match these curves with those of the fluorescing fractions from oat roots proved unsuccessful until we recently obtained a sample of scopoletin (6-methoxy-7-hydroxy coumarin or 6-methoxy-7-hydroxy 1:2 benzopyrone).



The pH-fluorescence curve of this compound had a shape very similar to that of one of our fractions (fraction *b*) from oat roots. A substance having some properties identical to those of scopoletin was then prepared from oat roots by a procedure recommended for the isolation of scopoletin.

**Method of Extraction.** The roots, amounting to 120 grams, were harvested from 3,300 five-day-old oat seedlings, *Avena sativa* var. Victory, germinated on filter paper in the laboratory. These were extracted by the method described by Best (1944). The roots were covered with 240 ml. of .05 N H<sub>2</sub>SO<sub>4</sub> and 100 ml. of chloroform and allowed to stand overnight. The chloroform was decanted and another 100 ml. of chloroform were added. After another twelve hours the second batch of chloroform was removed. The two chloroform fractions were combined and shaken repeatedly with 25 ml. portions of .005 M ammonium hydroxide. The ammonium hydroxide fractions were combined, acidified to about pH 2.5, and extracted with five portions of 50 ml. of chloroform. The chloroform fractions were then combined, dried over neutral calcium chloride, and filtered, and a small sample was removed for fluorometric study. The remainder was evaporated to dryness under vacuum. Approximately 3.8 mg.



of material were obtained. The residue was dissolved in 5 ml. benzene and put on a column of alumina 80 to 200 MM (alumina adsorption, Fisher Scientific Company). The brightly blue fluorescent material was strongly adsorbed at the top of the column and was washed repeatedly with benzene. The column was then washed with ethyl ether and subsequently with chloroform, but the fluorescent material remained at the top of the column during these washings. The alumina on which the fluorescent material was adsorbed was mechanically removed and eluted with .005 M ammonium hydroxide. The ammonium hydroxide was acidified to pH 3 and extracted with chloroform. The chloroform was dried over neutral calcium chloride, filtered, and the chloroform again evaporated under vacuum. The residue recovered by this procedure weighed 1.4 mg.

**Physical Properties.** *Absorption Spectra.* The absorption in the ultra-violet of the substance isolated from oat roots, as described above, was then compared with that of scopoletin. Our scopoletin sample, generously supplied by Dr. W. A. Andreae of the University of New Brunswick, was originally isolated from the roots of *Gelsemium sempervirens* and came from Dr. Léo Marion, National Research Council, Canada. The absorption curve of scopoletin (fig. 1) was measured in the spectral range between 210  $m\mu$  and 400  $m\mu$  at a concentration of  $2.5 \times 10^{-5}$  molar in 95 per cent ethanol, using a Beckman spectrophotometer. The measurements were made with the narrowest slit widths of the spectrophotometer and correction was made for the optical asymmetry of the "matched" quartz cells.

The substance isolated from oat roots was also prepared in ethanol at a concentration of 7.5 micrograms per milliliter. It was immediately obvious that the absorption curve was nearly identical with that of scopoletin. The assumption was then made that the impurities in the root extract did not absorb light at 347  $m\mu$  and the two curves were made to coincide at that wave length. When this was done, the curves differed by less than two per cent in absorption at wave lengths between 325 and 400  $m\mu$ . The difference between the curves increased steadily with decreasing wave-length. The extra absorption could be caused by a mixture of contaminating substances and shows only "end-absorption"—no peaks. If scopoletin is the substance in the root extract responsible for the 347  $m\mu$  peak, then 52 per

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#### Explanation of figures 1 and 2

FIG. 1. Absorption spectra (optical density as ordinate and wave length in millimicra as abscissa) of an alcoholic solution of scopoletin at a concentration of  $2.5 \times 10^{-5}$  molar (continuous curve) and of the root substance (circles). The two curves were made to coincide at 347  $m\mu$ . FIG. 2. Absorption spectra of scopoletin at a concentration of  $2.5 \times 10^{-5}$  molar (continuous curve) and of the root substance (circles) when measured in buffers with a pH of 0.3, 3.45, 7.67, and 10.0. The concentration of the root substance was such that the absorption at 347  $m\mu$  when measured in alcohol was the same as that of  $2.5 \times 10^{-5}$  molar scopoletin.



cent of the weight is scopoletin, and the other 48 per cent of the solids accounts for one-eighth or less of the total absorption at any wave length.

Qualitatively the two curves are strikingly similar with the peaks, valleys and plateaus occurring at identical wave lengths. The quantitative measurements on scopoletin are in good agreement with those of Andreae (1948).

The absorption spectra of scopoletin and the root extract in the region between 345 and 425  $m\mu$  (fig. 2) were measured in 1 N HCl (pH 0.3), in 0.1 M phosphate at pH 3.5 and pH 7.5, and in 0.5 per cent sodium bicarbonate-carbonate (pH 10.0). The scopoletin was measured at a concentration of  $2.5 \times 10^{-5}$  molar. The root substance was measured at the concentration that gave the same absorption in alcohol at 347  $m\mu$  as  $2.5 \times 10^{-5}$  molar scopoletin. The curves of both substances obtained at pH 0.3 and pH 3.5 were identical. The agreement in the other buffers is not as good, with deviations as large as 10 per cent. In general, the agreement is sufficiently exact to indicate that the absorption of the two solutions is due to the presence of the same or very closely related substances.

*Fluorescence.* The relationship between fluorescence and hydrogen ion concentration for scopoletin and for the root extract was determined by the method previously reported (Kavanagh & Goodwin 1949).<sup>1</sup> Sulfuric acid solutions of known normality (Michaelis & Granick 1942) were used to obtain pH values lower than 2. With a Corning 5970 lamp filter and a Corning 3060 + 3389 photocell filter, scopoletin at a concentration of 0.1  $\mu\text{g.}/\text{ml.}$  and the root extract at a concentration of 0.192  $\mu\text{g.}/\text{ml.}$  (a concentration which would show an absorption equal to that of 0.1  $\mu\text{g.}/\text{ml.}$  scopoletin at 347  $m\mu$ ) gave pH-fluorescence curves which were essentially identical. The potentiometer readings for the two substances were within the limits of experimental error at each pH. With the fluorimeter set to 100 with a 1  $\mu\text{g.}/\text{ml.}$  quinine sulfate standard, the scopoletin solution had a fluorescence of 189 at pH 9.35. The pH-fluorescence curves (fig. 3) obtained with a Corning 5860 + 738 lamp filter and a Corning 3060 photocell filter were also identical. Scopoletin at a concentration of 0.1  $\mu\text{g.}/\text{ml.}$  gave a reading of 148 under these conditions.

The identity of the two sets of pH-fluorescence curves indicates either that scopoletin and the root substance are identical or that the latter has exactly the same fluorescent efficiency as scopoletin and is quenched to the same extent by oxygen and by the buffer salts. Furthermore, the two substances show the same bright blue fluorescence throughout the pH range, and both decompose at the same rate in two buffers (pH 11.0 and 8.0), when irradiated by the 366  $m\mu$  lines of the mercury lamp.

<sup>1</sup> The Klett fluorimeter-colorimeter used in this investigation was purchased with a grant to the senior author from the Rumford Committee of the American Academy of Arts and Sciences.

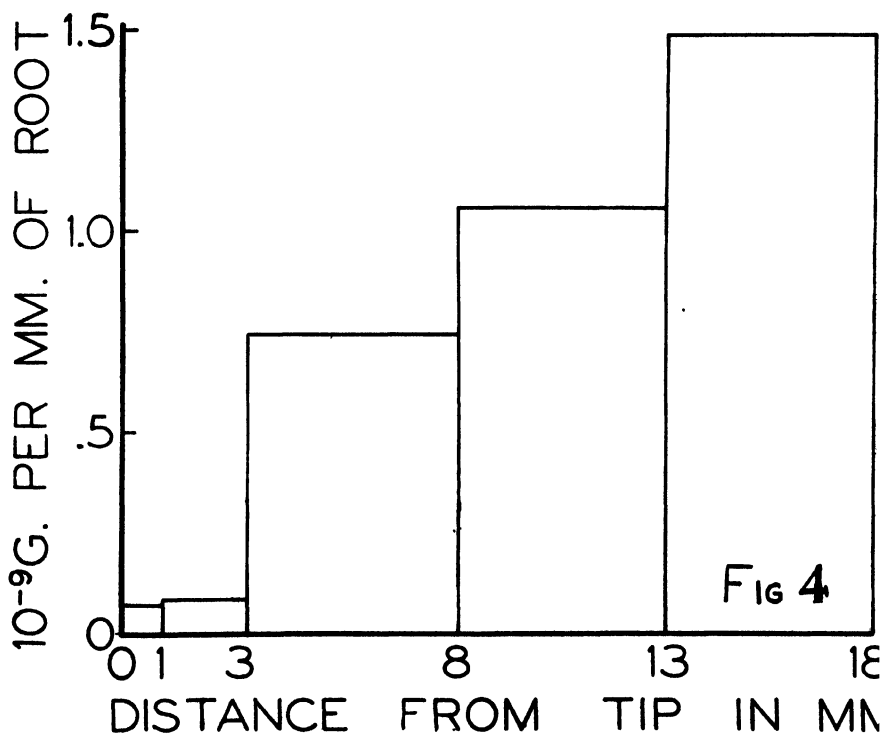
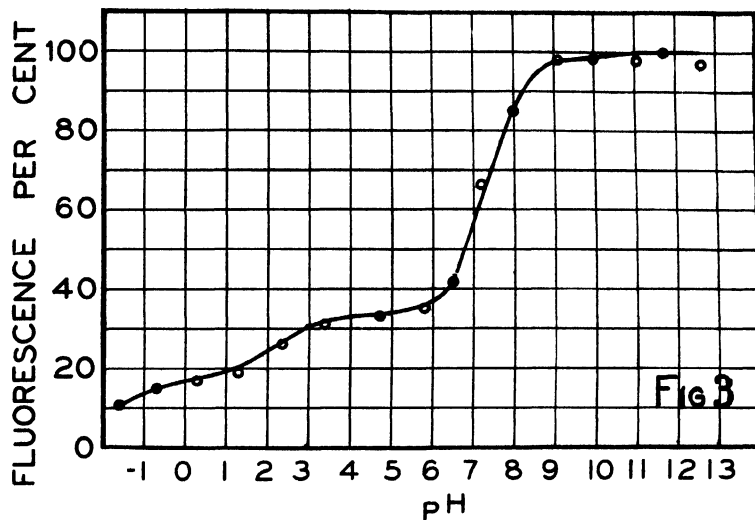


FIG. 3. The relationship between relative fluorescence and pH for scopoletin (continuous line) and for the root substance (circles). Lamp filter, Corning 5860+738; photocell filter, Corning 3060. FIG. 4. The distribution of scopoletin within the roots of 4-day-old *Avena* seedlings.

A study of the fluorescence of various coumarin derivatives is now in progress. Each compound thus far tested has proved to have fluorescent properties very distinct from those of scopoletin—even such closely related derivatives as umbelliferone, aesculetin, and aesculin. However, we have not yet been able to obtain the isomer of scopoletin (6-hydroxy-7-methoxy 1:2 benzopyrone) nor fabiatriin, the glucoside of scopoletin.

The foregoing optical data indicate that the root substance is scopoletin or a very closely related substance.

**Distribution of Scopoletin within the Plant.** It has been calculated that 0.38 microgram of scopoletin is present in the root-system of a five-day-old oat plant grown in the laboratory. This is approximately equivalent to 0.09  $\mu\text{g.}$  per root. In terms of wet weight, 10.43  $\mu\text{g.}$  of scopoletin per gram of root tissue were obtained. The calculation was based on the fluorescence of the small measured sample removed from the chloroform extract before evaporating to dryness. A pH-fluorescence curve of this sample was identical in shape to that of the final preparation, indicating purity with respect to the fluorescent material.

An experiment has been carried out to determine the distribution of scopoletin within the root (fig. 4). Roots from one hundred four-day-old plants were divided into five sections: (a) the terminal millimeter, comprising the rootcap and meristem; (b) the next two millimeters, including the region of cell elongation; and (c-e) the next 15 millimeters, divided into three equal sections. Each group of sections was ground up in 0.05 N sulfuric acid and the scopoletin was extracted, using essentially the same procedure as described above, except that much smaller quantities of reagents were used. The chloroform extracts were evaporated to dryness, and the fluorescent material was dissolved in water and measured in the fluorimeter. Enough material was obtained from the three groups of 5-mm. sections (c-e) to run pH-fluorescence curves. Those for the two basal groups of sections (d and e) were essentially identical in shape to that for pure scopoletin, but the apical 5-mm. group (c) had values somewhat too high in the acid range, indicating the presence in the extract of a fluorescing impurity. There was so little material in the apical three millimeters of the root (a and b) that the whole extract was used in each case for a single reading at pH 9.1. The fluorescence obtained may have been due in large part to substances other than scopoletin. The values given in figure 4, therefore, are probably fairly accurate for the two basal zones, but are almost certainly in excess of the true value for the three apical zones. The data show clearly that scopoletin is found predominantly in the maturer portions of the root and not in the growing regions.

A microscopic examination of living oat roots mounted in water was made using a dark-field condenser and the 366  $\text{m}\mu$  line from a mercury

are lamp. The meristematic region (the apical millimeter) was so brilliantly blue-fluorescent that histological detail was obscured. In the root-cap cells and epidermal cells adjacent to the meristem, the fluorescence was chiefly confined to the larger vacuoles and to smaller cellular structures which may have been vacuoles, plastids or mitochondria. The fluorescence of these smaller structures was often much more intense than that of the larger vacuoles. The cell walls were faintly bluish-fluorescent, while the cytoplasm and nuclei were dark. The fluorescent material can be readily extracted from the meristematic region with a number of solvents and gives a very distinctive pH-fluorescence curve, entirely different from that of scopoletin. This is the material which we have previously characterized as fraction *a* (Goodwin & Kavanagh 1948).

The older portions of the root show a much fainter bluish fluorescence, but if sodium carbonate buffer (pH 11) is drawn under the cover slip, a marked increase in this fluorescence is observed. Vacuoles of the root hairs and epidermal cells become a brighter blue, while the cell walls, which were a very faint blue in neutral solution, turn bright green. The increase in blue fluorescence of the cell contents under alkaline conditions is due to the presence of scopoletin. The green-fluorescing substance in the cell walls has yet to be identified.

**Discussion.** Coumarin and many of its derivatives such as umbelliferone, aesculetin, scopoletin, fraxetin, daphnetin, limettin and other more complicated compounds are frequently encountered as constituents of plants (see Sethna & Shah 1945). A number of the hydroxy coumarins occur as glucosides and, as such, may become important in the sugar metabolism of the plant. Aesculin, the glucoside of aesculetin, for example, has been found to constitute from four to five per cent of the weight of air-dried leaves of the Australian plant *Bursaria spinosa* (Dick 1943).

Scopoletin and its glucoside, fabiatriin (scopolin, murrayin), have been isolated from a number of species of flowering plants (table 1). The Solanaceae are particularly well represented. We believe that this is the first time scopoletin has been reported as having been isolated from monocotyledons, and we suspect that it may have a much wider distribution in plants than is indicated in table 1. Its presence is suggested by the shape of the pH-fluorescence curves of raw extracts of *Hordeum*, *Triticum*, and *Pisum* roots (Goodwin & Kavanagh 1948).

Scopoletin and its glucoside occur in many types of plant structures—leaves, stems, bark, flowers, tubers, and roots; but scopoletin seems to be most frequently accumulated in the roots. The histological distribution of blue-fluorescing material in the healthy tobacco plant is reported by Best (1948). He finds this fluorescence to be markedly brighter in the endodermis of the root-stock, stem, and leaf veins than in the other tissues of

these organs, while the small roots are fluorescent throughout. The blue fluorescence which he reports may not all be due to the presence of scopoletin, however.

In tobacco and potatoes scopoletin is produced in increased amounts as a consequence of certain virus infections. In tobacco infected with tomato spotted wilt virus, a blue fluorescence is found first as a halo in the mesophyll cells surrounding the lesions. Later the vascular tissue becomes fluorescent and still later scopoletin is accumulated in the roots (Best

TABLE 1. *The Occurrence of Scopoletin in Plants*

Family and species	Portion of plant	Author
Gramineae		
<i>Avena sativa</i> L.	Roots	Goodwin & Kavanagh (this paper)
Rosaceae		
<i>Prunus serotina</i> Ehrh.	Bark <sup>a</sup>	Power & Moore (1909)
Rutaceae		
<i>Chalcas exotica</i> (L.) Millsp. (= <i>Murraya exotica</i> L.)	Blossoms <sup>b</sup>	Blas (1868)
Loganiaceae		
<i>Gelsemium sempervirens</i> Ait. f.	Roots	Coblentz (1897), Schmidt (1898), Moore (1911), Seka & Kallir (1931)
Convolvulaceae		
<i>Convolvulus scammonia</i> L.	Roots	Power & Rogerson (1912)
<i>Ipomoea Purga</i> Hayne	Roots	Power & Rogerson (1910)
Solanaceae		
<i>Atropa Belladonna</i> L.	Whole plant ex- tracted	Kunz (1885)
<i>Fabiana imbricata</i> R. & P.	Leaves and twigs <sup>a</sup>	Kunz-Krause (1899), Edwards & Rogerson (1927)
<i>Nicotiana Tabacum</i> L.	Root, stem, leaf	Best (1944, 1948)
<i>Scopolia japonica</i> Max.	Roots <sup>a</sup>	Eijkman (1884), Henschke (1888)
<i>Solanum tuberosum</i> L.	Tubers	Andreae (1948)
Compositae		
<i>Artemisia</i> spp.		Sample from Wellcome Research Institution

<sup>a</sup> Also obtained as the glucoside.

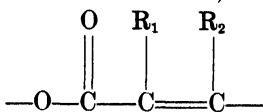
<sup>b</sup> Obtained as the glucoside.

1948). Scopoletin is found in potato tubers infected with leaf roll virus (Andreae 1948), the fluorescence occurring in cells adjacent to necrotic phloem tissue (Sanford & Grimble 1944). Diseased tubers can be quickly selected under ultraviolet light by examining the cut surfaces for fluorescence. The use of this technique in sorting seed potatoes may prove useful in reducing the incidence of infection by leaf roll and other types of virus (McLean & Kreutzer 1944).

From a quantitative standpoint it is interesting to note that scopoletin has been extracted in the following amounts: from *Fabiana imbricata* twigs, 1.4 mg. per gram of dried twigs (Edwards & Rogerson 1927); from *Gelsemium sempervirens* roots, 0.12 mg. per gram wet weight (Seka &

Kallir 1931); from diseased potato tubers, circa 0.01 mg. per gram wet weight (Andreae 1948); from *Avena sativa* roots, 0.01 mg. per gram wet weight.

Coumarin and its derivatives are among the compounds known as unsaturated lactones, which are characterized by the presence of the structure



within the molecule. These unsaturated lactones

have been shown to have physiological activity in many different kinds of organisms (Veldstra & Havinga 1945). In higher plants and bacteria they have been found to inhibit growth, and several of them are antibiotic substances. Parasorbic acid, one of the simpler unsaturated lactones, for instance, inhibits germination of seeds (Kuhn *et al.* 1943) and cell enlargement in the *Avena* coleoptile (Larsen 1947), while protoanemonin inhibits the growth of roots and slows down their metabolism (Goddard 1948). Some of the coumarins are still more effective inhibitors. Coumarin, aesculetin, and daphnetin inhibit seed germination (Cameron 1910; Sigmund 1914; Nutile 1945), while coumarin inhibits elongation (Audus 1948) and mitosis (Cornman 1946, 1947) in roots. Experiments now in progress indicate that scopoletin also inhibits the growth of roots at concentrations as low as  $10^{-5}$  molar.

Unsaturated lactones have been shown to react specifically with compounds containing the sulfhydryl ( $-SH$ ) radical (Cavallito & Bailey 1944; Cavallito & Haskell 1945). Since the presence of the sulfhydryl group has been found to be essential to cell proliferation (Hammett & Chapman 1938), the growth-inhibiting effects of the unsaturated lactones may well be due to the inactivation of sulfhydryl-containing enzyme systems. Thimann and Bonner (1949) have shown that the inhibiting action of protoanemonin and coumarin on growth is prevented by the presence of 2, 3-dimercaptopropanol, a compound known to protect sulfhydryl groups from inactivating substances. The unsaturated lactones are frequently found in physiologically significant concentrations within the tissues. Whether scopoletin acts as a natural growth regulator is not known, but the fact that it is present in mature portions of *Avena* roots at a concentration in excess of  $5 \times 10^{-5}$  molar, a concentration at least twenty times that found in the growing tip (apical three millimeters), is suggestive.

#### SUMMARY

The isolation and identification of one of the blue-fluorescing compounds in *Avena sativa* roots as scopoletin (6-methoxy-7-hydroxy coumarin) is reported. This substance is present in mature portions of five-day-old roots in concentrations in excess of 10 ppm. From three to 18 millimeters behind

the root apex, the amount of scopoletin per millimeter of root was found to lie between  $0.75 \times 10^{-9}$  and  $1.5 \times 10^{-9}$  gram. In the apical three millimeters, which includes the meristem and the region of cell elongation, the amount of scopoletin was too small to measure, but was certainly less than  $0.08 \times 10^{-9}$  gram per millimeter.

Published studies on the growth-inhibiting properties of coumarin and its derivatives are cited with reference to the possible role of scopoletin within the plant. In this regard the very low concentration of scopoletin in the actively growing portion of the root may be significant.

In this study, fluorescence has proved to be a very useful tool in locating, identifying and determining the amounts of scopoletin which are present in the plant.

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## NOTES ON THE CYTOLOGY OF SOME LYCOPSIDS

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A number of Wisconsin Lycopsids were investigated to determine somatic chromosome numbers and study peculiarities in somatic division.

Marquette (1907) first described spindle-formation as related to the plastids present in the young leaves of *Isoetes lacustris* L. (*Isoetes macrospora* Dur.) The presence of a single "starch body" (plastid) in each cell, the proximity of that "starch body" to the nucleus, its elongation and division before the prophase, the major role the daughter plastids play in spindle formation, and the persistence of the daughter "starch body" in the daughter cell were illustrated and described; its centrosome-like function was pointed out, and the name "polar structure" was suggested. Marquette concluded that ". . . it might possibly be assumed that in *Isoetes* we have a transition from a cell structure with well defined central bodies, as found in some algae and fungi, to a cell structure apparently without central bodies or anything corresponding to them as found in the spermatophytes."

Ma (1928) studied the chloroplasts of *Isoetes melanopoda* Gay & Dur. with reference to content and function during nuclear division. She found that the single plastid present in an embryonic cell lies in close contact with the nucleus and divides into two plastids which take polar positions during nuclear division. In some cells whose nuclei show no evidence of impending division two plastids were sometimes present, and in older cells and those exposed to light the plastids were more numerous.

Ekambaram and Venkatanathan (1933) discuss sporangium development and meiosis in the macro- and microsporangia of *Isoetes coromandelina* L. They found that in the heterotypic prophase " . . . the first visible change initiating division in the mother-cells is the appearance in the cytoplasm of a body very close to the nucleus. This is clearly made out when it forms a deep crescent adjoining the nucleus. It has a clear outline and appears to contain some dark staining granules of various sizes and other minute grains whose nature could not be made out with the methods of staining employed."

This structure referred to as a "polar body" divides to form four bodies which become arranged tetrahedrally near the periphery of the spore-mother cell. The relation of these four bodies to the formation of a tetrapolar spindle which becomes bipolar, their behavior during the division of nucleus and cell, the gradual decrease in size of the "polar body" present in each

young spore, and its ultimate disappearance in the fully developed spore are described. Similar bodies are met with also in the dividing vegetative cells. The chromosome count of *I. coromandelina* is given as  $n = 16$ .

Yuasa (1935) studying microsporogenesis in *Isoetes japonica*, finds the haploid number to be 33, and concludes that the species is a hexaploid. In his summary no mention is made of polar structures or of plastids, nor do the illustrations show them.

Ekstrand (1920) found the haploid chromosome number in *Isoetes echinospora* to be 11, the diploid 22. During the metaphases the spindle was sometimes seen to have two sharp-pointed poles, but centrosome-like bodies were not observed.

**Materials and Methods.** Root-tips, stem-tips, and strobili of *Lycopodium annotinum* L., *L. annotinum* var. *acrifolium* Fernald, *L. obscurum* L., *L. clavatum* L., *L. lucidulum* Michx., *L. inundatum* L., *L. Selago* var. *patens* (Beauv.) Desv., *L. complanatum* L., *Selaginella rupestris* (L.) Spring., *Isoetes macrospora* Dur., and *I. muricata* var. *Braunii* (Dur.) Reed, were collected in one or more of the Wisconsin counties: Vilas, Washburn, Langlade, and Sauk.

Material was fixed at the time of collection in Flemming's medium solution or in Randolph's or Belling's modification of Navashin's fixative. A cedar-anilin oil series or a terpineol series was used to avoid higher alcohols and chloroform.

Stains used were Heidenhain's iron-alum haematoxylin, Flemming's triple stain, and Crystal violet-iodine with picric acid as recommended by Smith (1934). Plants from which fixations were made were preserved as herbarium specimens.

**ISOETES.** A cell of any tissue in *Isoetes muricata* var. *Braunii* not too far differentiated to possess plastids at all, and if not actually dividing or preparing to divide, contains in general a single plastid (fig. 1). The description that follows applies particularly to cells of the root-tip.

A plastid is ellipsoidal to irregular in shape, about one-half to one-fourth the size of the nucleus, to which it is appressed. In the plane of contact the nuclear membrane may be flattened. The outer boundary of the plastid is membrane-like in appearance, often strikingly definite.

In preparations treated with iodine it usually can be seen that each plastid contains starch grains staining blue or brown; in crystal violet-iodine the grains are stained bright blue. The number in a plastid varies from two or three to fifteen or twenty. The starch grains are nearly spherical, ovoid, or disc-like. In the latter case they appear from oval to circular in surface view. They are not laminated; some possess a dark-staining cen-

tral hilum; others have a light-staining hilum and a darker margin. They vary greatly in size, the largest being five or six times the volume of the smallest. Plastids are present that contain very little starch, and others that include no starch. A plastid containing no starch can be distinguished only by careful observation and light-adjustment. The tiny starch grains when present can be shown to be optically active when between crossed polarizing screens.

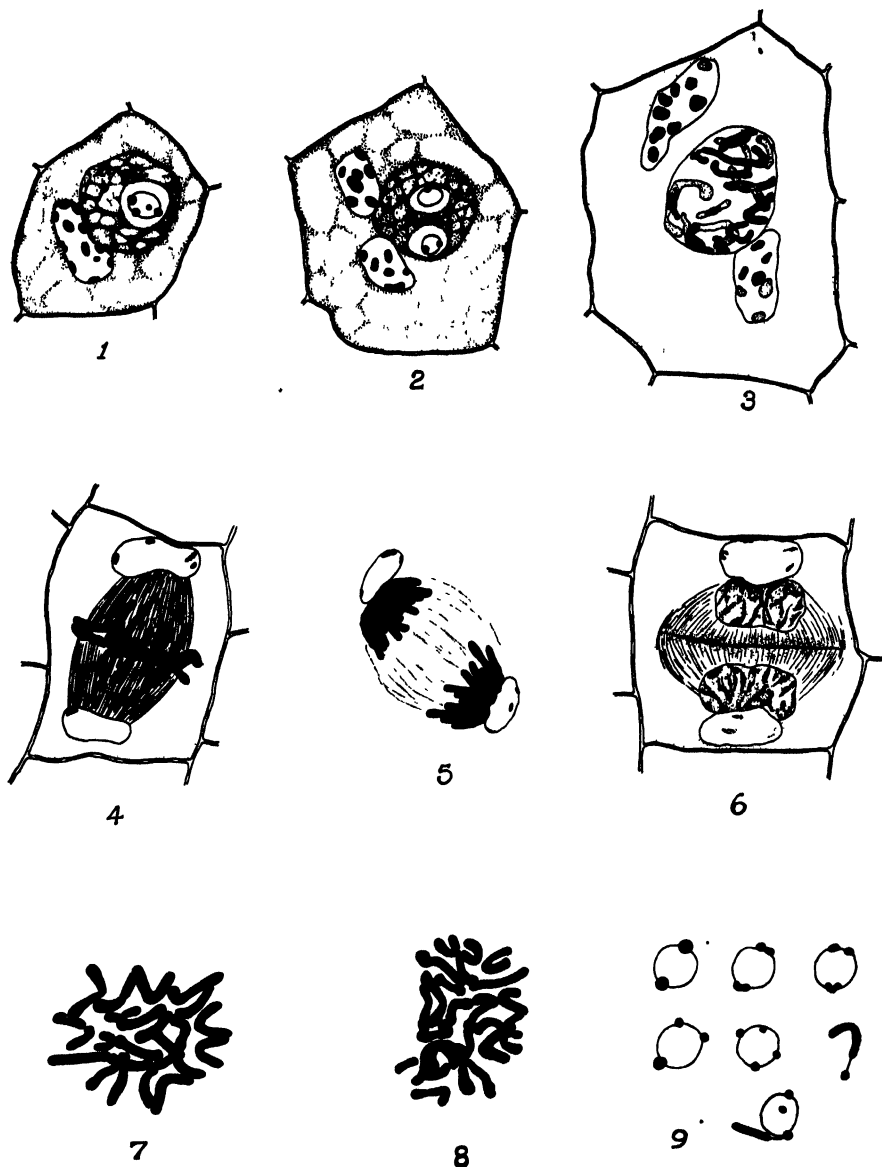
The single plastid present in an elongating and maturing cell may divide to form two or more daughter plastids (fig. 2). In such a case the plastids are commonly grouped about the nucleus; sometimes they appear in other parts of the cell. In maturing or mature cells plastids may be absent, or at least not detectable. These plastids are evidently similar to those first noted in young leaf cells of *I. macrospora* by Marquette (1907); he referred to them as masses of starch grains, each group apparently surrounded by a membrane.

Before the beginning of the prophase, the single plastid present in a meristematic cell elongates and finally divides; both ellipsoidal daughter halves then migrate until the two lie at opposite sides of the nucleus in contact with or close to the nuclear membrane (fig. 3). As the nuclear membrane disappears the plastids separate slightly and spindle fibers are seen to meet them along nearly half their proximal surfaces. The broad poles of the spindle are particularly evident during the equatorial plate stage (fig. 4) and the metaphases. When the plastids contain no visible starch they appear as vacuole-like structures at the poles of the spindle. However in some instances they may still be demonstrated because of their optically active contents.

During the late anaphases the shape of the chromosome group may be affected by the presence of the plastid; and the telophase daughter nucleus, in immediate contact with the plastid, is sometimes almost crescent-shaped (fig. 6). Nuclear division is followed by the formation of the cell plate which brings about the division of the cell (fig. 6). This history is similar to that reported by Marquette for the leaf cells of *I. macrospora*.

The nucleus of a resting meristematic cell occupies a central position and characteristically possesses one or two nucleoli which are left translucent by the crystal violet-iodine stain. Without exception, in all preparations made from variously fixed material, stained either with crystal violet-iodine or with the triple stain, a clear space is present about each nucleolus (figs. 1, 2).

In contact with the nucleolus, if a single one is present, two, three, or four highly chromatic bodies can be seen (fig. 9). They stand out sharply on the surface of the faintly stained nucleolus because of their chromatic nature. When two such bodies are present, they are spherical, slightly elon-



*Isoetes muricata* var. *Braunii*; cells in root-tip meristem. FIG. 1. Nucleus in very early prophase; single starch-containing plastid. FIG. 2. Nucleus in early prophase; two daughter plastids. FIG. 3. Late prophase; daughter plastids at opposite sides of nucleus. FIG. 4. Equatorial plate; plastids at spindle poles. FIG. 5. Plastids in contact with anaphase chromosome groups. FIG. 6. Plastids in contact with telophase nuclei. FIGS. 7, 8. Equatorial plates; showing 24 and 25 chromosomes. FIG. 9, a-e. Satellites in contact with nucleolus. f. Chromosome with satellite. g. Nucleolus with satellite chromosome.

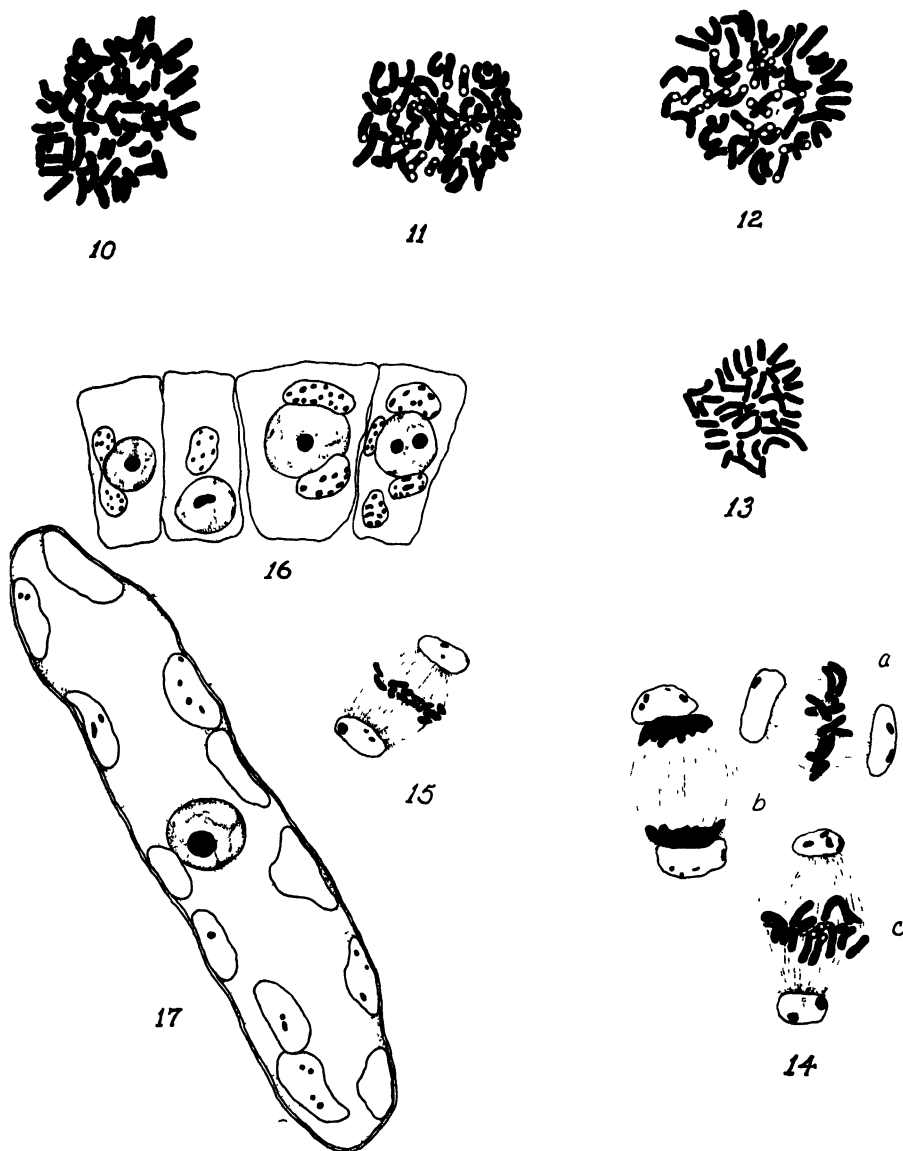


FIG. 10. Equatorial plate of *L. clavatum* var. showing 60 chromosomes. FIG. 11. Equatorial plate of *L. obscurum* showing 50 chromosomes. FIG. 12. Equatorial plate of *L. annotinum* showing 50 chromosomes. FIG. 13. Equatorial plate of *L. complanatum* var. *elongatum*; 40 chromosomes. FIG. 14, a, c. Equatorial plates on *L. complanatum* var. *elongatum* showing plastids at the spindle poles. b. Plastids in contact with anaphase chromosome groups of *L. complanatum* var. *elongatum*. FIG. 15. Exceptionally large figure in *Selaginella rupestris* showing plastids at spindle poles. FIG. 16. Plastids containing red-staining granules in tapetal cells of *S. rupestris*. FIG. 17. Chloroplasts containing red-staining granules in leaf cell of *S. rupestris*.

gated, or dumbbell-shaped; when four bodies are present each is smaller than in the case of two; they may lie in pairs or separated by variable distances. The different degrees of separation observed suggest that the four bodies result from the division of the two sometimes seen. When two nucleoli are present each bears on its surface one or two chromatic bodies (fig. 2). These bodies, as the later history shows, are the satellites borne on at least one pair of chromosomes. When the nucleus enters the prophase and the chromosomes become clearly recognizable, two chromosomes visibly connected with the satellites by means of delicate fibers have been observed. Each satellite chromosome is attached to one undivided satellite (fig. 9), or to an already divided one which appears as two. Certain identification of one satellite chromosome (fig. 9) was made in two separate equatorial plates; in most plates, however, their identification is prevented by the length and curvature of the chromosomes.

After the completion of nuclear division, as the daughter nuclei grow and become nearly spherical, a nucleolus appears, and, in contact with it, the two satellites; or if two nucleoli are present, one satellite is in contact with each.

Chromosome counts made in cross sections of root tips of *I. muricata* var. *Braunii* show the diploid number to be 24–26 (figs. 7, 8). The chromosomes vary in length, most of them being long, and on some the position of the centromere to which the spindle fiber is attached is recognizable. There is some tendency for similar chromosomes to lie near together in the equatorial plate, but the appearance is confused by their length and curvature.

In *I. macrospora* the structure and behavior of the plastids are essentially as in *I. muricata* var. *Braunii*. Here, however, the poles of the spindle are not broad, but sharply defined points, each of which occupies a slight hollow in the surface of the corresponding plastid. This condition was noted in cells of young leaves, and in meristematic stem tissue. Roots of *I. macrospora* have not been examined. This species has approximately twice as many chromosomes as *I. muricata* var. *Braunii*; the material available has not made a count possible.

**SELAGINELLA.** In the tapetal cells in the micro- and macrosporangia of *Selaginella rupestris* (fig. 16), in other cells of the sporangium, frequently in embryonic and elongating stem cells, and in leaf and ligule primordia, leucoplasts are present which differ from the chloroplasts in cells of the stem and leaves in size and in staining reaction. Each cell contains one or two, occasionally three or four leucoplasts. These bodies are from spherical to ellipsoidal in shape and usually smaller than the nucleus, about 5 to 6  $\mu$  in diameter; they usually lie in contact with or close to the nucleus, but sometimes appear in other parts of the cell. A leucoplast has a distinct

outer margin, suggesting the presence of a limiting membrane. Within the leucoplast, when stained with the triple stain, are seen from 2 or 3 to 15 or 20 small red granules. The granules vary somewhat in shape, usually being spherical or ellipsoidal, sometimes more elongated. All are of approximately the same size, about  $1\ \mu$  in diameter; they do not turn blue in the presence of iodine and are optically inactive.

Ma (1930) has described the chloroplasts of *Selaginella* with special reference to those in the leaf cells of *S. apoda* . . . "in which a single plastid is found in most cells. . . . By the time the leaves have reached a length of 0.2 mm., spindle-shaped red-staining bodies are clearly recognizable in the plastids . . . as the plastids enlarge with the increase in size of the cells, the bodies, which stain red with the triple stain, also increase in size." Ma noted blue-staining starch grains also in the same plastids, the starch grains being of the same shape and size as the red-staining bodies. In some plastids, bodies were present whose staining reaction was intermediate between that of the red bodies and the starch grains. The red bodies gave a positive protein reaction with Millon's reagent, since it appeared that these red-staining bodies in the plastids of *S. apoda* may be transformed into starch grains, it was suggested that they are similar in nature and function to the pyrenoid bodies of *Anthoceros* and *Notothylas* (McAllister 1926).

The chloroplasts of *Selaginella rupestris* (fig. 17), most easily studied in the leaves, are ellipsoidal. Each contains from one to five or six spherical red-staining bodies similar to those in the leucoplasts. None of my preparations show anything in either chloroplast or leucoplast that would suggest a transition from the red-staining bodies to blue-staining starch grains. Each of the many chloroplasts in a leaf cell (fig. 17) is about  $3\ \mu$  in width and  $6\ \mu$  in length. The red granules vary in size from about 0.5 to  $1\ \mu$ , whereas starch grains present in the plastids vary from about 0.5 to  $3.5\ \mu$  in diameter. From the staining reactions of the isotropic granules in the chloroplasts it seems evident they are not starch; it is possible that they are proteinaceous in nature.

Division figures were noted in cells of *S. rupestris* in which one plastid occupied each pole of the spindle (fig. 15), but these figures were too few in number to justify a statement on the behavior of the plastid during division. The diploid chromosome count is more than 12.

**LYCOPODIUM.** In young sporangia of *Lycopodium complanatum* var. *elongatum* in which premeiotic nuclear divisions are occurring, sporogenous cells not dividing or preparing to divide contain, as a rule, a single leucoplast. The plastid is elongated, appressed to the nucleus, and contains variable numbers of starch grains. The grains, which turn blue in the presence

of iodine and stain bright blue with crystal violet-iodine, are similar in shape to those described in *Isoetes muricata* var. *Braunii*, and number commonly from 2 or 3 to 10 or 15 in each plastid. Some plastids contain very little starch; in some starch is entirely absent. The latter plastids appear like vacuoles. The plastid in a cell whose nucleus is in the very early pro-phases is elongated; somewhat later it divides to form daughter plastids the starch content of each of which is approximately half that of the original plastid. The two daughter plastids come to lie on opposite sides of the nucleus and in close contact with the nuclear membrane. Some cells have been seen which contained more than two plastids, two of which lie at opposite sides of the nucleus, the others lie near the plasma membrane.

At the equatorial-plate stage, at which time the typical broad poles of the spindle can best be seen (fig. 14, *a, c*), in preparations stained with crystal violet-iodine, starch grains are usually visible at each pole of the spindle; careful observation shows that they lie within a plastid apparently bounded by a membrane. During the metaphases, anaphases (fig. 14 *b*), and telophases likewise, a starch-containing plastid can usually be seen at each broad pole of the spindle. If starch is absent, the plastid at each pole appears much like a vacuole. Thus it is evident that, as in the embryonic root-tip cells of *Isoetes muricata* var. *Braunii* and in embryonic leaf and stem cells of *I. macrospora*, the single plastid present in a sporogenous cell of *Lycopodium complanatum* var. *elongatum* divides to form two daughter plastids which function in the formation of the spindle and which occupy the spindle poles during nuclear division, persisting during the telophases and in the daughter cells.

Chromosome counts made in root tips showed the diploid number to be 40 (fig. 13). The chromosomes of this species as seen in the equatorial plate are all rather short.

Premeiotic nuclear divisions in sporogenous tissue of *L. obscurum* show in some cases a plastid at each spindle pole. This condition was noted in a few equatorial-plate figures and in a few anaphases. In all these cases starch grains were present in each plastid. However, in the material studied so little starch was present that plastid identification was often uncertain.

Chromosome counts were made from cross sections of rhizome tips and from sporangia. The diploid chromosome number is about 50 (fig. 11). The chromosomes vary greatly in length, some being short but the majority rather long. The length of the chromosomes is not so evident in polar views as in lateral views of equatorial plates. In the latter, the long arms of some of the chromosomes reach almost to one or the other spindle pole.

In root tips of *L. annotinum*, each embryonic or elongating cell possesses from one to 8 or 10 plastids. A plastid is ellipsoidal to spherical in shape and contains in addition to starch grains from 2 or 3 to 15 or 20 granules



which vary little in size. These granules are similar to those present in *Selaginella rupestris*; like those, they take a red color in the triple stain. The plastids usually lie appressed to the nucleus, and if sufficiently numerous they may completely surround the nucleus. Staining reactions supply no evidence that the red-staining granules change to starch. The starch grains are present in the same plastids with the red-staining granules, are from 4 to 6 times their diameter, and are blue with the triple stain. Whether or not the red granules are in any way related to starch formation is uncertain.

In preparations stained with iron-alum haematoxylin the plastids are clearly visible and the included starch grains are from gray to black. No structures appear that correspond to the red-staining granules, so conspicuous with the triple stain. In haematoxylin-stained preparations the membrane-like outer boundary of the plastid is readily recognizable, the starch grains lying in close contact with it.

The chromosomes of this species vary from 3 to 5  $\mu$  in length; their curvature and crowding make counting difficult. The diploid number is about 50 (fig. 12).

In root-tip preparations of *L. clavatum* stained with iron-alum haematoxylin, plastids, one or two in each cell, appear similar to those of *L. annotinum*. They are in contact with the nuclear membrane and contain from gray to black starch grains similar to those of *L. annotinum*. In equatorial-plate, metaphase, anaphase, and telophase stages, the starch grains are visible at spindle poles, and often it is evident that the grains lie within a plastid. Here, then, as in *L. complanatum* var. *elongatum*, it appears that the plastids function in the formation of the achromatic figure and that they occupy the poles of the spindle during nuclear division.

The diploid chromosome count is about 60 (fig. 10). Counting is made difficult, as in *L. annotinum*, by the curvature and crowding of the chromosomes.

The chromosome numbers of *L. inundatum* and *L. lucidulum*, studied in the root-tips, seem to be approximately the same as *L. clavatum*. Similarities to *L. clavatum* appears also in the sizes and shapes of the chromosomes. Mitotic figures were too crowded for a satisfactory count of the chromosomes. In root-tip cells of *L. inundatum* and *L. lucidulum*, starch-containing plastids were observed apparently similar to those of *L. complanatum* var. *elongatum* and *L. obscurum*.

**Conclusion.** If a single plastid present in any embryonic cell divides to form two daughter plastids which function in the formation of an achromatic figure, occupy the spindle poles during nuclear division, and persist in the daughter-cells, the entire sequence of events may be spoken of as

plastid-polarity. Somatic and meiotic plastid-polarity are convenient terms to designate in which type of tissue this polarity is exhibited.

Similar somatic plastid-polarity has been shown to exist in *Isoetes macrospora* (Marquette 1907), *I. melanopoda* (Ma 1930), *I. coromandelina* (Ekambaram 1933), and *I. muricata* var. *Braunii* (herein reported). Meiotic plastid-polarity is shown to be present in *I. coromandelina* (Ekambaram 1933). The function of plastids in spindle-formation and their presence at the poles of the spindle during nuclear division in these four species suggest the possibility of their occurrence and like function in other species of *Isoetes*.

In *Selaginella rupestris* a few figures were seen in which a plastid was present at each pole of the spindle.

TABLE 1. *Chromosome Numbers in the Lycopsiida*

Species	Number reported		Author
	<i>n</i>	<i>2n</i>	
<i>Isoetes coromandelina</i>	16		Ekambaram & Venkatanathan 1933
<i>I. echinospora</i>	11		Ekstrand 1920
<i>I. asiatica</i>		22	Takamine 1921
<i>I. japonica</i>		43-45	Takamine 1921
<i>I. japonica</i>	33		Yuasa 1935
<i>I. muricata</i> var. <i>Braunii</i>		24-26	Dunlop
<i>Selaginella Vogeli</i>		16	Heitz 1925
<i>S. Ouvardii</i>		20-22	Heitz 1925
<i>S. Martensii</i>		52-57	Heitz 1925
<i>S. grandis</i>		16-17	Heitz 1925
<i>S. emiliana</i>	8		Denke 1902
<i>S. serpens</i>	8		Denke 1902
<i>S. rupestris</i>		12 +	Dunlop
<i>Lycopodium clavatum</i>	14		Baranov 1925
<i>L. clavatum</i> var.		ca. 60	Dunlop
<i>L. complanatum</i> var. <i>elongatum</i>		40	Dunlop
<i>L. annotinum</i>		ca. 50	Dunlop
<i>L. obscurum</i>		ca. 50	Dunlop

Somatic plastid-polarity has been described above in the premeiotic nuclear divisions of *Lycopodium complanatum* var. *elongatum*; the condition is similar to that in *Isoetes*. In *L. obscurum* premeiotic figures were seen that strongly suggest polarity. In embryonic root cells of *L. annotinum*, starch-containing plastids were seen at the spindle poles in division figures.

The occurrence of somatic plastid-polarity in both *Isoetes* and *Lycopodium*, and perhaps also in *Selaginella* is significant.

Starch-containing plastids were observed in all species studied. Plastids containing granules colored red in the triple stain were seen only in *Selaginella rupestris* and *Lycopodium clavatum*. The nature of the red-staining granules is not clear. Similar granules present in *Selaginella apoda* were thought by Ma (1930) to have a pyrenoid-like function.

Chromosome size within the Lycopsidea (in those species studied) varies from the extremely small and short chromosomes of *Selaginella rupestris*,  $1\ \mu$  or less in length, to the large, long chromosomes of *Isoetes muricata* var. *Braunii* which may be  $0.5\text{--}1\ \mu$  in thickness and 7 or  $8\ \mu$  long. Chromosomes of *Lycopodium complanatum* var. *elongatum* are about  $0.5\ \mu$  in thickness and  $1\text{--}3\ \mu$  long. Those of the other species of *Lycopodium* studied are intermediate in length between those of *L. complanatum* var. *elongatum* and *Isoetes muricata* var. *Braunii*, and are from 1 to  $1.5\ \mu$  in thickness. Satellite chromosomes were seen in preparations of *Isoetes muricata* var. *Braunii*, but not in the other species studied.

#### SUMMARY

In *Isoetes muricata* var. *Braunii* plastids function in the formation of the achromatic figure and occupy the spindle poles during nuclear divisions in the meristem of the root tip.

*Isoetes muricata* var. *Braunii* possesses at least one pair of satellite chromosomes.

Red-staining granules of uncertain function are present in chloroplasts and leucoplasts of *Selaginella rupestris*. Similar bodies were observed in leucoplasts in root cells of *Lycopodium annotinum*.

Plastid behavior during premeiotic nuclear division in *Lycopodium complanatum* var. *elongatum* is similar to that during nuclear division in *Isoetes muricata* var. *Braunii*. In *Lycopodium obscurum* and *L. clavatum* evidence of plastid behavior like that in *Isoetes muricata* var. *Braunii* is strong.

Chromosome size and number in some Wisconsin species of the Lycopsidea have been determined.

The author is indebted to Dr. Charles E. Allen for his constructive criticism.

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POSTGLACIAL FORESTS IN WEST CENTRAL  
ALBERTA, CANADA<sup>1</sup>

HENRY P. HANSEN

Peat sections were obtained from four bogs along the Edmonton-Jasper highway in west central Alberta. These bogs lie at distances of about 30, 55, 85, and 125 miles west of Edmonton. More specifically they are located about 4 miles north of Duffield, 4 miles east of Entwistle, near the town of McKay, and about 5 miles west of Edson, respectively. Hereafter they will be referred to as the Duffield, Entwistle, McKay, and Edson sections or bogs. All sites lie within the westernmost border of the Keewatin drift. Although the Cordilleran glaciers descended the east slope of the Rocky Mountains in this latitude, the relationships between the two ice sheets and the borders of their drifts are uncertain. It is evident, however, that the Keewatin ice was more extensive in this region, because the Cordilleran glaciers were probably limited by the relatively low precipitation on the east slope of the mountains. One stage of the Cordilleran glaciers descended the eastern flanks of the Rockies to points 50 miles east of the mountains in the vicinity of Calgary, and still farther east in the latitude of Edmonton (Flint 1947). During one or more stages the Cordilleran and Keewatin ice may have coalesced, but there is no evidence that their fronts were joined during the Late Wisconsin (Mankato) stage in west central Alberta. It seems probable that the last glacier in the region was of Keewatin origin. Keewatin boulders have been noted as far west as Edson, although no end moraines have been observed in this area (Erdtman & Lewis 1931). The eastern border of the Altamont moraine, which is dated as terminal Late Wisconsin, lies about 75 miles east of Edmonton (Bretz 1943). It is considered to be equivalent to the Mankato maximum of the Minnesota-Iowa region. West of the Altamont moraine in the general latitude of Edmonton are older Keewatin moraines. The westernmost and oldest of these is the Duffield moraine, whose eastern border lies about 25 miles west of Edmonton. Although the Duffield moraine is older than the Altamont, its topography is much more youthful than the Early Wisconsin (Iowan) drift in Montana (Bretz 1943). In a previous paper (Hansen 1949) it was suggested that the Duffield was equivalent to the Tazewell or Cary of the eastern ice, although geologists have not recog-

<sup>1</sup> The author is grateful to the American Philosophical Society for a grant from the Penrose Fund to defray the expenses of the field work, to the John Simon Guggenheim Foundation for a fellowship during 1947-48, to the General Research Council of Oregon State College for a grant for laboratory assistance, and to Dr. John Merkle, Texas A. and M. College, for assistance in the field work.

nized an intermediate Wisconsin stage for the western ice (Antevs 1945). Lying between the Duffield and the Altamont moraines are the Buffalo Lake and Viking moraines which are younger than the former but older than the latter (Bretz 1943). If the uppermost drift for 200 miles west of the Altamont is of Keewatin origin, but older than the Altamont, there must have been an ice-free area which may have been forested during the Late Wisconsin glaciation. The possibility that bogs lying between Edmonton and the westernmost border of the Keewatin ice on the east flank of the Rockies are pre-Late-Wisconsin is supported by the fact that the Keewatin ice retreated downslope so that the meltwater was ponded against the ice and drained laterally. This may have eliminated a long period of physiographic instability which would have hindered the formation of permanent basins in which hydrarch succession took place. There is greater possibility that meltwater from the Cordilleran glacier, flowing eastward, may have destroyed or buried sites of pre-Late Wisconsin bogs, or on the other hand prevented hydrarch succession and the deposition of pollen-bearing sediments during the Late Wisconsin stage near the mountains. The pollen record in peat sections west of the Altamont moraine, however, suggests that forests did exist in this ice-free area at least during the latter part of the Late Wisconsin.

**Characteristics of the Bogs.** All the bogs are in the mature stage with climax forest trees on their surfaces. Sphagnum moss and Labrador tea (*Ledum groenlandicum*) and other species of ericaceous plants cover the bogs, with local areas of sedges and other hydrophytic species. Trees on the muskegs include black spruce (*Picea mariana*), tamarack (*Larix laricina*), and lodgepole pine (*Pinus contorta*), the latter being absent on the Duffield bog. Bog birch (*B. glandulosa*) is very common, and in some areas is more abundant than Labrador tea. Other muskegs in the area were noted that supported dense forests of large black spruce and some white spruce (*Picea glauca*), suggesting that hydrarch succession had been terminated for some time, perhaps owing to the age of the bog or the shallowness of the depression. The depth of the bogs in the area of sampling is as follows: the Duffield, 3 m.; the Entwistle, 6.5 m.; the McKay, 1 m.; and the Edson, 7.0 m. In the Duffield and Edson sections, almost a meter of clay at the bottom was devoid of pollen. In the Entwistle section, volcanic glass was identified at 3 and 3.2 m. and at 0.6 m. In the Edson section, glass was noted from 4.2 to 4.6 m. and at the surface. The source of the ash is not certain, but some of it may have come from Glacier Peak in north central Washington, while some may have been derived from the west, possibly the Coast Range of British Columbia. It seems probable that the glass near the surface came from the eruption of Mt. Katmai in Alaska in 1912. This is supported by the occurrence of volcanic glass in the upper levels of peat sections from many bogs

along the Alaska highway in northeastern British Columbia. It is possible that the glass at the 3 m. level in the Entwhistle section is synchronous with the 4.4 m. horizon in the Edson column, as suggested by their respective trends of forest succession.

The relative depths of the bogs provide no criteria with respect to their relative ages. If the area in which the bogs are located was not influenced by the Cordilleran ice of the Late Wisconsin glaciation, then it could be assumed that the westernmost was the oldest. On the other hand, if the Cordilleran ice succeeded the Keewatin, particularly in the western portion, the Edson bog might be considered the youngest. This possibility is supported by its formation in a river valley which carries water from the mountains to the west. During melting of the Cordilleran ice, the valley probably carried considerable more water than it does at present, thus preventing hydrarch succession until the stream had subsided. The relative stratigraphic position of the volcanic glass and the pollen profiles suggests that the Edson section is younger than the other thick section near Entwhistle.

In preparation of the peat for pollen analysis, the potassium hydrate method was used. Pollen is abundant except in the inorganic, clay sediments underlying the organic peat, which suggests absence of forests in the region when these accumulated. From 100 to 200 pollen grains of forest trees were identified at each level. An attempt was made to separate lodgepole from jack pine and white spruce from black spruce by their pollen size ranges. In interpreting the pollen profiles, however, it was found to be infeasible to use the species separately, because of the many sharp fluctuations from level to level, which could not be ascribed to any logical cause.

**Forests of the Region.** In the general vicinity of Edmonton occurs the meeting place of three climax vegetation formations of North America. These are the boreal forest, the Cordilleran forest, and the grasslands (Lewis et al. 1928). Lying between the grasslands and the boreal forest to the north and the Cordilleran forest to the west is a transition zone known as the Parkland because of the scattered groves of trees, consisting largely of aspen (*Populus tremuloides*) in the southern part, and aspen, white spruce, white birch, and balsam poplar (*P. tacamahacca*) in the northern part. Moss (1932) divides the Parkland into a northern Poplar area and retains the name Parkland for only the southern third. He also divides the grassland into a northern and southern prairie. The occurrence of black and brown soils in the Poplar area and Parkland as well as podsolized prairie soils in the southern fringe of the boreal forests suggests greater extension of grassland in the past, perhaps during the warm, dry maximum between 8,000 and 4,000 years ago (Hansen 1947, 1949).

The arborescent species of the boreal forest are black and white spruce,

balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), tamarack, aspen, balsam poplar, and white birch. White spruce and its varieties are the most abundant, widespread, and permanent, and in the absence of fire and cutting they become the climax dominants except in the northern part of their range where black spruce and tamarack invade higher ground and act like climax dominants, and in certain local areas. Balsam fir also may be considered a climax species, although it is not so abundant as white spruce, and probably does not range west of north central Alberta (Halliday & Brown 1943). Jack pine is subclimax on burns and assumes a climax role on sandy areas in the white spruce forest. Lodgepole pine replaces jack pine in the boreal forest in western Alberta, British Columbia, and the Yukon. Their ranges overlap within 20 miles west and northwest of Edmonton and throughout the Peace River and Lesser Slave Lake regions.<sup>2</sup> Unlike jack pine, lodgepole often invades mature bogs with black spruce, tamarack, and white birch. Aspen, poplar, and white birch form a fire subclimax associates throughout the boreal forest of Alberta and British Columbia, with either jack pine or lodgepole pine, depending upon the location and soil.

The Cordilleran forest is included in the Petran subalpine and Petran montane forests (Weaver & Clements 1938), which extend along the crest and the upper slopes of the Rockies. It extends eastward from the mountains, forming a narrowing wedge reaching almost to the center of the province of Alberta. The arborescent species of the Cordilleran forest in Alberta include subalpine fir (*Abies lasiocarpa*), which replaces balsam fir of the boreal forest, Engelmann spruce (*Picea engelmanni*), lodgepole pine, and aspen. Whitebark pine (*Pinus albicaulis*), limber pine (*P. flexilis*), and Douglas fir (*Pseudotsuga taxifolia*) occur in the southern part of the Cordilleran forest in the mountains. White spruce ranges throughout the Cordilleran forest southward into Montana (Munns 1938), while both tamarack and black spruce are common on muskegs in the more northern part. Aspen, poplar, and white birch also occur abundantly in the Cordilleran forest, where aspen is the most abundant because of its invasion of burns. At present, however, the predominant forest species in the Cordilleran forest of Alberta is probably lodgepole, which occupies burns and other edaphically disturbed areas, either initially or with aspen. Lodgepole also becomes progressively more abundant westward toward the Rockies.

The easternmost bog of this study is located in the western part of the Poplar area, while the other three lie within the Cordilleran forest. Lodgepole is not common in the vicinity of the easternmost bog, but it becomes progressively more abundant westward. Grassland openings are common.

**Postglacial Forest Succession.** The pollen profiles indicate that pine and spruce have been the principal species in the region throughout the time

<sup>2</sup> Information from Professor E. H. Moss, University of Alberta.



represented by the sedimentary columns (figs. 1, 2, 3, 4). At most levels, they constitute more than 90 per cent of the total tree pollen. It is unfortunate that aspen pollen is so poorly preserved, because this species undoubtedly played an important part in postglacial forest succession, as is suggested by its present proportions in the Cordilleran and boreal forests. Its invasion of

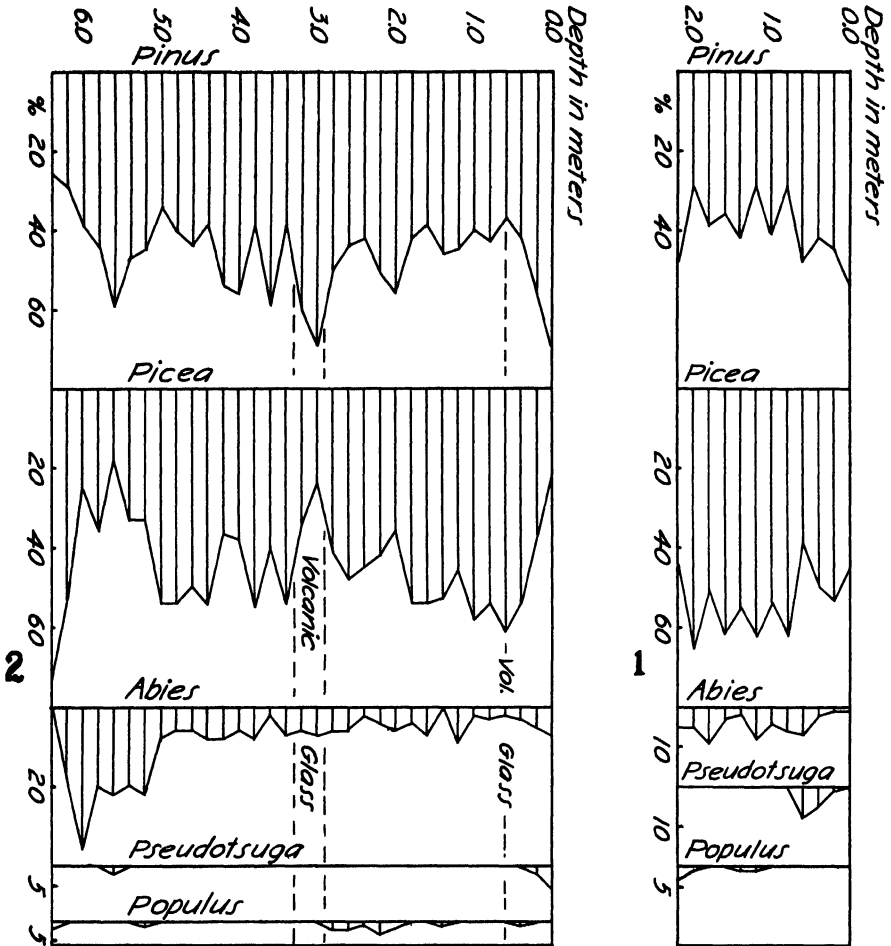


FIG. 1. Pollen diagram of the Duffield bog. FIG. 2. Pollen diagram of the Entwistle bog.

white spruce of lodgepole burns suggests that its postglacial record in conjunction with that of spruce and pine would reflect periodic pyric influence more than climatic trends. The interpretation of the pollen profiles largely upon the basis of competition between pine and spruce may not present a true picture of the relative influence of climate and fire on adjacent forest

successions. Practically all of the pine pollen was identified as lodgepole, and interpretation of the profiles is based upon this species. Both black and white spruce pollen was separated in significant proportions, but their individual profiles apparently do not present a true picture of their relative importance in upland forest and bog succession. Black spruce pollen should logically increase in proportion in the upper levels of the peat sections because of its invasion of the mature bog, but there is no consistent pattern of relative proportions of black and white spruce in this respect. Incompetency of the size range method in separating these two species may be responsible for this anomaly. In general, however, white spruce pollen is more abundant than that of black spruce throughout the sedimentary columns, suggesting that the presence of white spruce in adjacent upland forests had a greater influence upon the relative amounts of the two species of pollen in the peat.

Interpretation of the pollen profiles must be based largely upon pine and spruce fluctuations, although some fir pollen is present and its profiles provide a definite trend. Fluctuations of spruce and pine have been largely opposite to each other throughout, indicating their reciprocal successional relationships, perhaps in response to fire and edaphic disturbances, or on mature bogs (figs. 1, 2, 3, 4). The many sharp, opposite fluctuations from level to level fail to present a trend denoting that some consistent, regional influence was at play. Also, the lack of correlative over-all trends in the four sections does not provide either regional patterns or a progression of some influence in an east-west axis that might have been caused by increase in elevation westward or the relative influences of the Keewatin ice advancing from the east and the Cordilleran glacier moving outward on the east slope of the Rockies.

In the Duffield section, spruce has been largely predominant throughout, with pine gaining a slight advantage near the top, which may reflect the influence of fire since the advent of white man (fig. 1).

In the Entwistle section, which is the deepest, spruce is predominantly recorded at the bottom with 74 per cent, which is its maximum of all profiles (fig. 2). Throughout the section, however, pine and spruce fluctuate conversely to each other, which may be attributed to local periodic fires, disease, or variables inherent in the method of pollen analysis. The only suggestive trend is the maximum of pine attained at 3 m., the same level at which volcanic glass occurs, which may represent the influence of the climatic maximum between 8,000 and 4,000 years ago. A decline of pine above this level may reflect an increase in moisture, while a sharp increase of pine at the top may record the effects of burning augmented by white man.

In only the McKay section is lodgepole predominantly recorded at the bottom in significant proportions (fig. 3). It remains predominant throughout, which may reflect the influence of large adjacent sandy areas on which lodgepole forms dense, pure stands.

The Edson section, which is almost as thick as the Entwistle column, perhaps shows more definite trends than the others. Pine and spruce are about equal at the bottom, but spruce increases and pine declines in the next

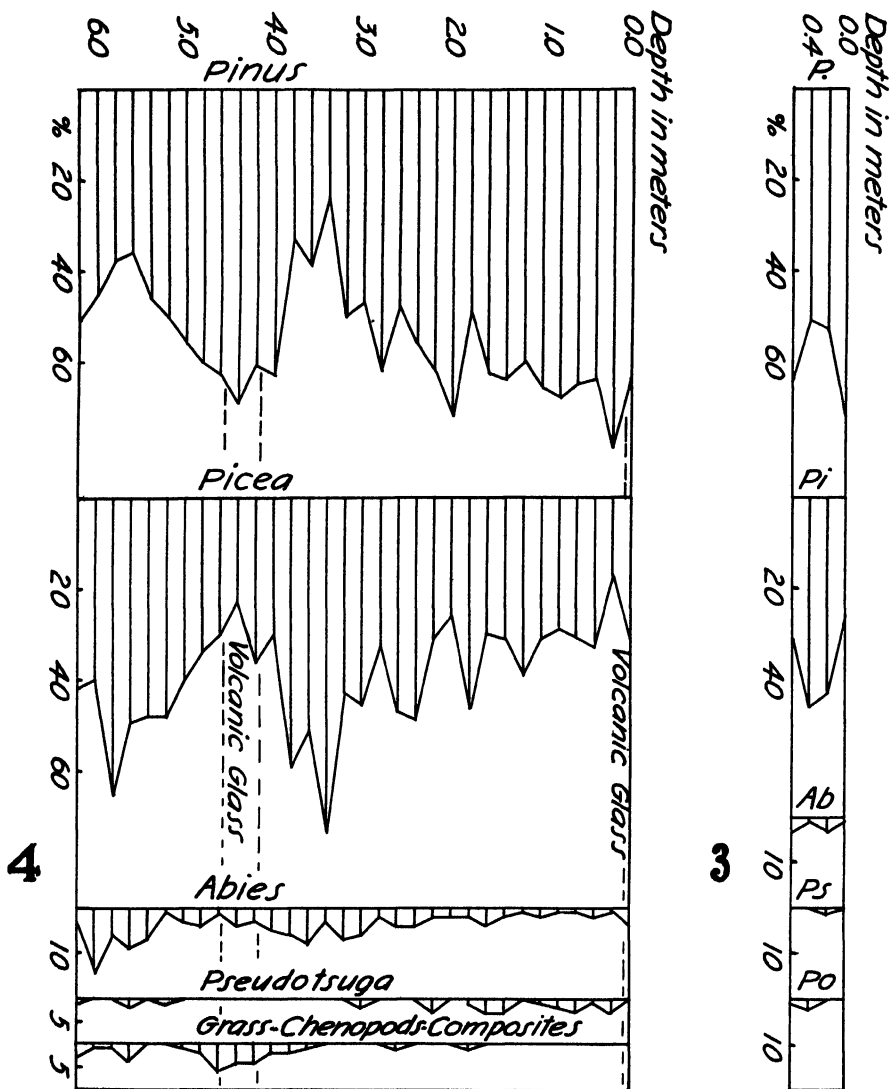


FIG. 3. Pollen diagram of the McKay bog. P, *Pinus contorta*; Ab, *Abies*; Pi, *Picea*; Ps, *Pseudotsuga taxifolia*, PO, aspen. FIG. 4. Pollen diagram of the Edson bog, showing volcanic glass layer\*through grass maximum.

few levels (fig. 4). They reverse their trends with pine rapidly expanding to 69 per cent and spruce diminishing to 23 per cent at 4.4 m., at which horizon

volcanic glass was noted. If this is chronologically correlated with the 3 m. level in the Entwistle sections where glass also occurs, this increment in pine may reflect a decrease in moisture. A third sharp reversal of trends reveals a decline of pine to 24 per cent at 3.4 m., its lowest point of the profile, and an increase in spruce to 73 per cent, its highest proportion. From these horizons, pine gradually expands and spruce reciprocally declines toward the top, where they are recorded as 64 and 32 per cent respectively, again perhaps representing the influence of fire and the general over-all more favorable conditions for lodgepole pine at higher elevations toward the Rocky Mountains. If the Edson and Entwistle sections are chronologically correlated by their respective volcanic glass levels at 4.4 and 3.0 m. respectively, either the Edson column is younger than the other or the rate of peat deposition has been considerably slower in the former, as the ratio of thickness below the glass is almost 1:2. It has been suggested that the Edson section is younger than those farther east, perhaps because of its proximity to the Cordilleran glacier and the resultant physiographic instability during glacial retreat, accentuated by the site of the Edson bog in a valley. On the other hand, it implies a more rapid rate of peat deposition above the glass horizon in the Edson bog, which might be attributable to moister climate nearer the mountains.

The profiles of fir, representing largely subalpine fir, show a consistent trend which may be of some climatic significance (figs. 1, 2, 3, 4). In the Edson and Entwistle sections, fir is best represented near the bottom, and attains its maxima a few levels higher. From these maxima, fir declines in both sections to proportions less than 10 per cent at the top. As the present range of subalpine fir indicates that it likes a cold climate, its greatest representation near the bottom suggests a cooler climate at that time than now exists. Its higher proportions in the Entwistle section throughout, however, is inconsistent with the present range of fir. It becomes more abundant westward at higher elevations in the Rockies and one would logically expect it to be better represented in the Edson section, which is nearer the mountains. The higher proportions of fir in the lower horizons of the Entwistle section suggest that the Edson section is younger. Fir may have existed in greater abundance farther east in ice-free areas during the Late Wisconsin, before the more western Edson bog had initiated pollen-bearing sedimentation. By this time, conditions had become more favorable for spruce, with which fir could not compete.

The occurrence of ice-free areas west of the Altamont border during the Late Wisconsin, as indicated by forest composition, is further supported by the pollen profiles of several bogs east and south of Edmonton. In six of seven sections, pine is predominant when pollen-bearing deposition began (Hansen 1949). These bogs lie east of the lodgepole pine range and most of

the pine pollen in the lower levels was identified as jack pine. This record is quite different from that in the Great Lakes region and eastern North America, where spruce is consistently recorded as the predominant, pioneer, postglacial invader of deglaciated moraine, with the exception of north-western Wisconsin, where jack pine was apparently co-abundant with spruce on sandy soils (Wilson 1938). These spruce forests with some fir, were replaced by pine as the climate became warmer and drier. This anomaly might be explained by one or more of the following causes and conditions. First, the pollen record does not include the earliest post-Altamont forests which may have consisted largely of spruce and fir, owing to a more rigorous climate. Second, spruce forests may have existed in adjacent ice-free areas before and during the Altamont stage, but conditions favored pine expansion so that it was still predominant when the earliest pollen-bearing sediments were deposited. Third, if the pollen profiles are entirely post-Altamont, the edaphic conditions may have been more favorable for pine than spruce because of physiographic instability resulting from the nearby glacier. Fourth, the early post-Altamont climate may have been milder and drier here than in the Great Lakes region and farther east. Fifth, strong prevailing westerly winds may have carried pine pollen from the Cordilleran forest, where conditions for pine expansion and persistence had been favorable longer.

In this study, however, a somewhat different analogy must be employed, because most of the pine pollen apparently is that of lodgepole pine. In the Pacific Northwest, pollen analysis of many peat sections reveals that lodgepole was consistently the predominant, pioneer, postglacial invader of deglaciated terrain (Hansen 1947). While the ecologic requirements of lodgepole and jack pine seem to be somewhat similar, their relationships to the climax species in their respective areas seem to be slightly different. Both thrive as a result of fire and edaphic disturbance, but lodgepole seems to have a greater ecologic amplitude and is better able to replace the climax dominants. Its range also suggests that it can stand a more rigorous environment than jack pine, while its invasion of mature bogs suggests it has a wider range of soil tolerance. Because of these characteristics, lodgepole is not so good a climatic indicator as jack pine with respect to their respective climax dominants. In the Pacific Northwest, it seems probable that early postglacial physiographic and edaphic instability was favorable for lodgepole in the absence of competition by Douglas fir and western hemlock (*Tsuga heterophylla*). In western Alberta, however, the postglacial co-abundance of pine and spruce, the latter a climax dominant, may represent edaphic and pyric influence more than climatic. Both the sandy or gravelly soil and frequent fires have been favorable for the persistence of lodgepole in abundance. It should be mentioned, however, that with species of wide geographic range,

ecologic races with different ecologic amplitudes may well exist. The abundance of lodgepole pine in west central Alberta peat sections may not mean the same as its early postglacial predominance in the Puget Sound region. Its predominance on sterile pumice mantles in the Oregon Cascades would seem to be more nearly analogous to its co-abundance with spruce in west central Alberta.

The abundance of lodgepole pine when the earliest pollen-bearing sediments were deposited tends to support Hultén's theory that arctic and boreal floras had their greatest spread from centra in Beringia south and east into North America largely by the time of the Yarmouth interglacial (Hultén 1937). They survived the Illinoian and Wisconsin glacial stages in ice-free areas either at the perimeter of the glacier or possibly within the glaciated region. As the glaciers receded, the plants invaded deglaciated terrain from these refugia. Lodgepole pine is considered to be one of a group of continental western American radiants that had migrated south of the 40 parallel and had re-established itself northward by the time of the Late Wisconsin. During this last glacial stage it may have survived in the ice-free corridor between the Cordilleran and Keewatin glaciers. That it also survived in abundance immediately south of the Late Wisconsin ice border in the Puget Sound region and eastern Washington is well evidenced by its preponderant pollen representation at the bottom of many peat sections from these areas (Hansen 1947). Subalpine fir is also classified as a continental western radiant species and its appreciable proportions in the lower levels of all sections further supports its pre-Late-Wisconsin persistence on the east slope of the Rockies in west central Alberta. Neither of these species has spread very far east, and their interglacial and postglacial migrations have apparently been north-and-south and confined largely to the Rockies and the Coast Ranges. Raup (1947) would include *Picea glauca* and *P. mariana* with Hultén's continental western American radiants, but it seems probable that they found refuge south of the ice largely east of the Rockies and spread both east and west during pre-Late-Wisconsin interglacial stages. During at least the latter part of the Late Wisconsin glaciation, lodgepole and spruce occupied the ice-free area on the east slope of the Rockies in west central Alberta, and fire and edaphic disturbance occurred at sufficiently close intervals to favor the persistence of a high proportion of lodgepole in the forest complex.

Other conifers represented sporadically and sparsely in the peat sections include Douglas fir and tamarack. The latter is poorly represented considering its abundance on the bog surface. Douglas fir pollen probably drifted considerable distances, largely from the Rockies, where it occurs as far north as Jasper. It is most consistently recorded in the Edson section, which is to be expected because of its proximity to the mountains (fig. 4). *Populus* is

also sporadically recorded, but in insufficient proportions to be of any interpretive significance except that the pollen of this species is poorly preserved in peat. Fairly high proportions of *Populus* pollen were noted in a few bogs about Edmonton (Hansen 1949). Pollen identified as that of poplar occurs in all but the Edson bog, and this is also consistent with the composition of adjacent forests, as lodgepole becomes more abundant farther west at the expense of aspen. In the Edson section, the author was surprised to note grass, chenopod, and composite pollen in many levels, with grass the most common (fig. 4). It may be merely coincidental, but the volcanic glass which has been tentatively assigned to Glacier Peak which apparently erupted near the time of the postglacial climatic maximum as indicated by many pollen profiles in Washington, occurs at the same levels as the grass maximum. As the climatic maximum in eastern Washington is portrayed by a sharp influx of these drouth indicators, it may be possible that the influence of this warm, dry interval was felt in west central Alberta. A significant maximum of this group of xeric indicators also occurs in the peat sections east and south of Edmonton, which further supports this evidence.

#### SUMMARY

Pollen analysis of four peat sections from bogs lying between Edmonton and the Rockies in west central Alberta, reveal that lodgepole pine and spruce have been the predominant forest tree species in adjacent areas during the time represented by the sedimentary columns. Since these bogs lie west of the border of the Altamont (Late Wisconsin) moraine and on older Keewatin drift, but probably east of the Late Wisconsin Cordilleran ice border, it is possible that they record pre-Late-Wisconsin forests, that had persisted in an ice-free corridor during this glacial stage. This is consistent with Hultén's theory that continental western American radiants from a Beringia center had migrated southward before the Wisconsin glaciations and persisted ice-free areas close to or within the ice front during at least the Late Wisconsin stage. The postglacial warm, dry interval, evidenced from so many sources, may be slightly recorded by an influx of grasses with some chenopods and composites in the vicinity of the Edson bog, 125 miles west of Edmonton.

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## NOTE ON THE SECTION MICROPHYLLAE OF AGROSTIS

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At the time of the original description of the section *Microphyllae* Beetle of *Agrostis* (Bull. Torrey Club **72**: 541-549. 1945) all known species with awned glumes were treated. It was found that two other characters, a bent, exserted awn and absence of the palea, were correlated with the awning of the glumes. Since 1945 two new species have been described which would fall into the section *Microphyllae* of *Agrostis* with the exception that both have well developed paleae.

*Agrostis aristiglumis* Swallen (Leaf. West. Bot. **5**: 56. 1947), which falls well within the geographic range of the four species originally listed, is unquestionably a member of the section, and requires the emending of the original concept of the section to include both the presence and absence of a palea.

*Deyeuxia parsana* Bor (Kew Bull. **1948**: 42. 1948) also described with awned glumes—"ab omnibus speciebus adhuc descriptis glumis aristatis facile distinguitur"—undoubtedly belongs in the same section. It is a perennial described from "Persia. Shah Zadeh Kuh, 3100 m., coll. Dr. A. Parsa Typus in Herb. Kew." and extends the range of the section into the Old World for the first time. Like *Agrostis aristiglumis* Swallen this species has an exserted awn of the lemma and a well developed palea. In order to place it properly in a section of *Agrostis* the following transfer is made: *Agrostis parsana* (Bor) Beetle, comb. nov.

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NEW SPECIES OF CYPERACEAE FROM BRITISH  
GUIANA AND SURINAM

CHARLES L. GILLY

From among the specimens of northern South American Cyperaceae examined during the past year,<sup>1</sup> the following three species merit recognition.

## TRIBE HYPOLYTREAE

\* *Hypolytrum sandwithii* Gilly, sp. nov. Herba perennis, caespitosa?; caulis brevis lignosus; folia lineari-elliptica glabra (concolora?), 5-6 dm. longa and 2.3 cm. lata, margine minute serrulata, basi in petiolum canaliculatum attenuato, ad apicem longe acuminata, acumine ad 1 dm. longo; culmi floriferi solitarii in axilibus foliorum, subtriangulares glabri vel minute pulverulentes et supra ad angulos minute serrulati, cum inflorescentia 2-3 dm. alti; inflorescentia subcorymbosa, spiculae glabrae in glomerulis dispositae; glomeruli 0.8-1.2 cm. diam., solitarii ad apices ramulorum ad 2 cm. longorum, glomerulo ultimo sessili; bracteae inferiores inflorescentiam subtendentes foliis consimiles, ad 2.5 dm. longae; bracteae superiores glomerulos subtendentes lanceolatae acuminatae ad 1.5 cm. longae; flores in spiculis bisexualibus monoecis; spiculae bracteolis hyalino-brunneis lanceolatis vel oblongo-lanceolatis acutis vel obtusis ad 2.5 mm. longis subtentae; glumae hyalino-brunneae glabrae; glumae vacuae exteriores 2, subcarinatae lanceolatae vel elliptico-lanceolatae, 3-3.5 mm. longae; glumae flores masculos subtendentes planae lineari-lanceolatae vel anguste lanceolatae, ad 2.5 mm. longae; flores masculi 4-6 monandri in parte spiculae inferiori, perianthio nullo, antheris ad 1 mm. longis, filamentis persistentibus; flores feminei in parte spiculae superiori et media, perianthio nullo; achaenium subteres vel subtereti-lenticulare subulato-conicum, ad 1 mm. latum et cum rostro spongioso glabro et persistens 4-5 mm. longum; corpus achaenii stramineo-olivaceum, cum rostro minute et dense purpureo-maculatum; stylus bifidus, stigmata gracilia atro-brunnea. BRITISH GUIANA: Potaro River, Kaieteur Falls: by stream in high forest, descending from savanna to falls, "growing with spp. of Rapateaceae . . . only this specimen collected; no others seen with inflorescence," altitude ca. 400 m., September 5, 1937, *N. Y. Sandwith 1379* (K—TYPE; NY—drawing and fragment; ISC—photograph and fragment).

<sup>1</sup> Specimens reported upon in this paper may be found in the herbarium of the Royal Botanic Gardens, Kew, England (K) or in the herbarium of the New York Botanical Garden (NY), and duplicates or photographs and accompanying fragments are in the herbarium of Iowa State College (ISC); isotypes of the two members of the Cryptangieae presumably have been distributed to still other herbaria. I wish to express my thanks to the curators of these herbaria for permission to examine the specimens, and to offer particular thanks to Mr. N. Y. Sandwith for his courtesy in referring the specimen of *Hypolytrum* to me for study and for his patience in awaiting determination.

In the structure of the achene beak, this species apparently is related to *H. strictum* Kunth (see Clarke 1909, *pl. 103, f. 18*), and in the type and arrangement of leaves it is very similar to *H. Jenmani* C. B. Clarke; however, *H. sandwithii* differs markedly from both of these species in the details of inflorescence, spikelets and achenes. The long-acuminate leaf apices are distinctive in the genus. It is of interest to note that *H. sandwithii* greatly resembles some of the species of the related genus *Bisboeckelera* Kuntze, particularly *B. irrigua* (Nees) Kuntze of northwestern Brazil and *B. longifolia* (Rudge) Kuntze of Surinam and French Guiana.<sup>2</sup>

#### TRIBE CRYPTANGIEAE

***Cephalocarpus maguirei*** Gilly, sp. nov. Caulis multiramosus ad 1.5 dm. altus, foliis persistentibus tectus; folia linearia acuta bicarinata glabra margine costaque albo-pilosulis et carinis uncinato-papillois exceptis, ad 5 cm. longa et 2 mm. lata; culmi floriferi solitarii in axilibus foliorum, 4.5–6 cm. alti; bractee inflorescentiam subtendentes ciliatae et 8 mm. longae; spiculae masculae 3.5–4 mm. longae, glumis vacuis 3–5 lanceolatis acutis vel mucronulatis glabris, glumis staminiferis 2–3 lanceolatis acutis glabris; antherae deciduae ignotae; spiculae femineae 3.5–4 mm. longae, glumis 5–8 ovatis vel lanceolato-ovatis mucronatis glabris; achaenia subteretia glabra atrobrunnea ad 1.5 mm. longa et 1 mm. diam., rostro 0.5–0.7 mm. longo luteo glabro deciduo, apiculo 0.1–0.2 mm. longo; squamellae hypogynae minute orbiculares, ciliis paucis longitudine partem tertiam corporis achaenii aequantes. BRITISH GUIANA: Kaieteur savannas, "forming tussocks . . . rare. . . ." May 14, 1944, *B. Maguire and D. B. Fanshawe 23453* (NY—TYPE).

A member of the subgenus *Neocephalocarpus* by virtue of the solitary flowering culm in each leaf axil. Characters of the achene and the deciduous beak, however, have been observed previously only in the subgenus *Eucephalocarpus*; an eventual realignment of the intrageneri subdivisions of *Cephalocarpus* (Gilly 1942) may be in order. This specimen has been previously recorded (Svenson 1948) in the literature as "*Cephalocarpus* aff. *rigidus* Gilly."

***Everardia surinamensis*** Gilly, sp. nov. Caulis gracilis, ad 8 cm. altus, vaginis persistentibus brunneis fimbriatis tecta; folia plana glabra margine costaque albo-pilosulis exceptis vel subtus sparse pilosula, ad 3.5 dm. longa et ad basim 1 cm. lata; culmi floriferi minute pubescentes laxe adscendentes

<sup>2</sup> Although superficially resembling and first placed in the Cariceae, *Bisboeckelera* has been assigned by various authors to the Cryptangieae, the Sclerieae or to the Bisboeckelerieae. Its affinities, however, are with *Hypolytrum*, *Mapania*, and related genera of the Tribe Hypolytreae; the utriole ("false perigynium" of some authors) of *Bisboeckelera* apparently has been developed through embryonic coalescence, or failure of embryonic separation, of sterile glumes such as occur between the staminate flowers and the pistillate flower in *Lepironia*, *Mapania*, and *Thoracostachyum*. The relationships in this complex will be considered in detail at a later date. The genus *Bisboeckelera* has been discussed at length by both Standley (1914) and Pfeiffer (1937).

vel erecti, cum inflorescentia ad 4 dm. alti; vagina ad basim 3 cm. longa; vaginae floriferae brunneae minute pubescentiae laminas subaequant; spiculae masculae numerosae 3–4 mm. longae, glumis vacuis 3–6 ovatis vel ovato-lanceolatis acutis vel mucronatis glabris, glumis staminiferis 3–5 lanceolatis vel oblongo-lanceolatis acutis vel mucronulatis glabris; spiculae femineae 2.8–3.2 mm. longae, glumis 5–6 ovatis vel ovato-triangularibus mucronatis; achaenia brunnea anguste ellipsoidea, ad apicem sparse et minute pubescentia, cum rostro 2.5–2.8 mm. longa, 0.5 mm. diam.; rostro conico pubescenti, quam corpore achaenii dimidio brevioribus; squamellae hypogynae minutae suborbiculares, ciliis paucis quam corpore achaenii brevioribus. SURINAM: Tafelberg (Table Mountain): wet places in dense low makka swamp, near Savanna no. IV, altitude 520 m., August 15, 1944, *B. Maguire* 24382 (NY—TYPE); moist mossy rocks, base of wall, West Escarpment, altitude 485 m., September 10, 1944, *B. Maguire* 24679 (NY).

Vegetatively similar to *E. montana* Ridley (see Gilly 1940) from Mount Roraima and Ptari-tepui in Venezuela, as previously indicated by Svenson (1948), but differing greatly from that species in structure and pubescence of the achene as well as in minor vegetative characteristics.

It is also of interest to note that a staminate specimen of the genus *Didymiandrum* [BRITISH GUIANA: savannas on the Kaieteur plateau, May 5, 1944, *B. Maguire* & *D. B. Fanshawe* 23230 (NY)]—appears to be more nearly referable to *D. guaiquinimae* Schnee (Schnee 1943) than to *D. stellatum* (Böckl.) Gilly, as recently reported by Svenson (1948). *D. guaiquinimae*, originally described from pistillate plants collected on Cerro Guaiquinima in southeastern Venezuela, has been collected more recently by Steyermark on Ptari-tepui, another cerro in the same area.

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**NOWAKOWSKIELLA CRASSA SP. NOV., CLADOCHYTRIUM  
AUREUM SP. NOV., AND OTHER POLYCENTRIC  
CHYTRIDS FROM MARYLAND<sup>1</sup>**

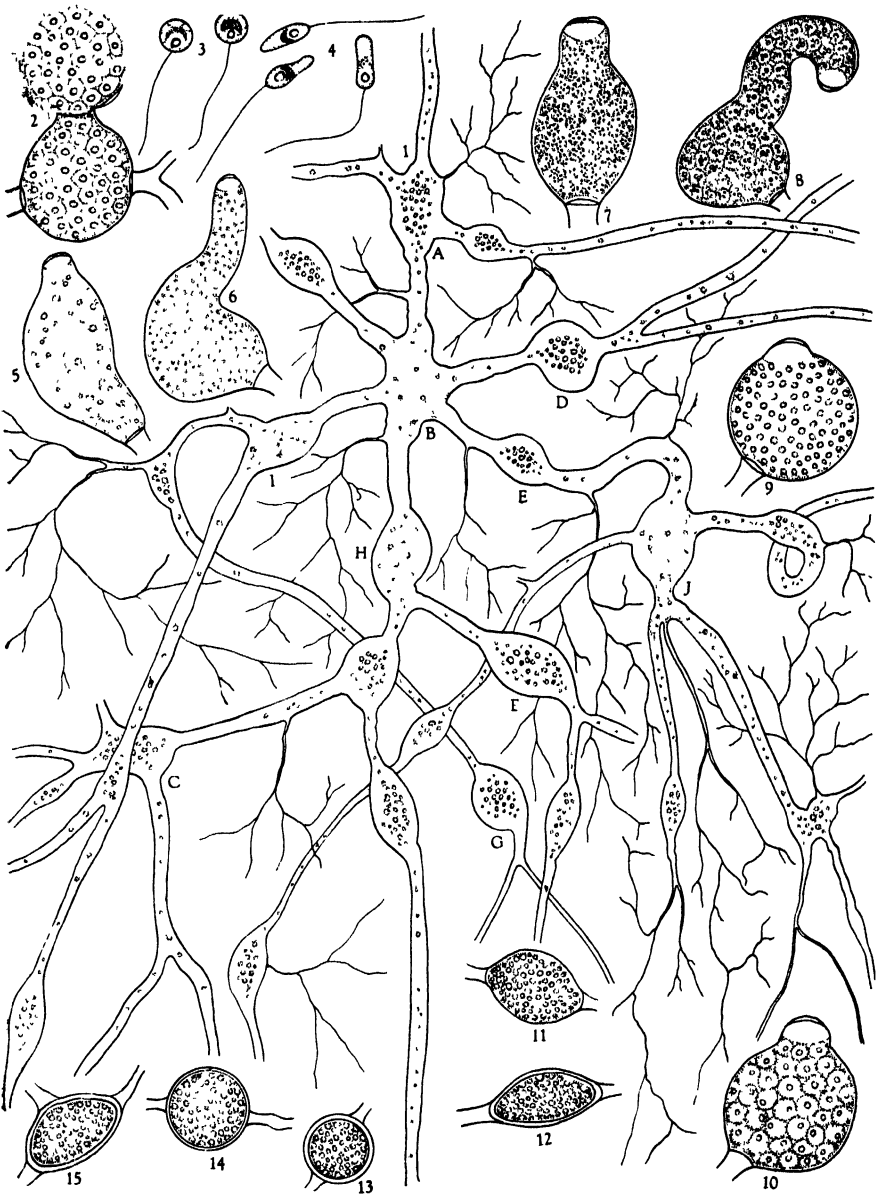
JOHN S. KARLING

In the course of a survey of the soil fungi of Maryland a number of polycentric chytrids were isolated on cellulosic, chitinic, and keratinic substrata, and among these were two new species of the family Cladochytriaceae. Both of these chytrids were isolated from a mixture of soil and water and grown on floating bits of onion scale. It was found later, however, that they may grow to some extent on dead human skin also, but not on chitin. The first of these species is characterized by an usually large and coarse rhizomycelium without pseudosepta or trabeculae, nonseptate intercalary swellings, and operculate sporangia, and belongs in the genus *Nowakowskiella*. It differs fundamentally from the other species of this genus by its exceptionally large thallus, and for this reason it is diagnosed as a new species and named *N. crassa*. The second species is distinguished by a very delicate rhizomycelium, septate intercalary enlargements, and inoperculate sporangia. Accordingly, it belongs in the genus *Cladochytrium*, and is strikingly similar to *C. tenue* in most respects. However, it differs from this species by its larger zoospores and the presence of a highly refringent golden-orange to red globule in the latter. In this respect its zoospores resemble those of *C. replicatum*, but otherwise the two species appear to be different and distinct. The Maryland species is, therefore, interpreted as a new species for which the name *C. aureum* is proposed.

***Nowakowskiella crassa* Karling, sp. nov.** Fungus saprophyticus. Rhizomycelio hyalino, profuso, ramoso, partibus tenuibus 6-18 $\mu$  diam., incrementis pluribus non septatis, subsphaericis, 14-21 $\mu$ , ovalibus, 12-18  $\times$  16-22 $\mu$ , fusiformibus, 14-16  $\times$  25-28 $\mu$ , aut irregularibus. Sporangiiis terminalibus aut intercalaribus, hyalinis, levibus, sphaericis, 15-40 $\mu$ , ovalibus, 18-30  $\times$  22-38 $\mu$ , fusiformibus, clavatis, aut irregularibus; operculo 10-15 $\mu$  diam. Zoosporis sphaericis, 4.5-5 $\mu$  diam. unico globulo refringenti, 0.8-1.2 $\mu$  diam; flagello 24-26 $\mu$  longo. Sporis perdurantibus hyalinis, levibus, sphaericis, 12-23 $\mu$ , ovalibus, 18-20  $\times$  22-24 $\mu$ ; germinatione ignota.

Saprophytic in dead and disintegrating vegetable debris, small brook on route 506 near Prince Frederick, Calvert County, Maryland.

<sup>1</sup> This work was begun at the Chesapeake Biological Laboratory, Solomons, Md., where the writer was guest investigator during the spring and early summer of 1948. The author is deeply indebted to the Department of Education and Research, State of Maryland, and particularly to the Director of the Laboratory, Dr. R. V. Truitt, for providing research facilities and funds.



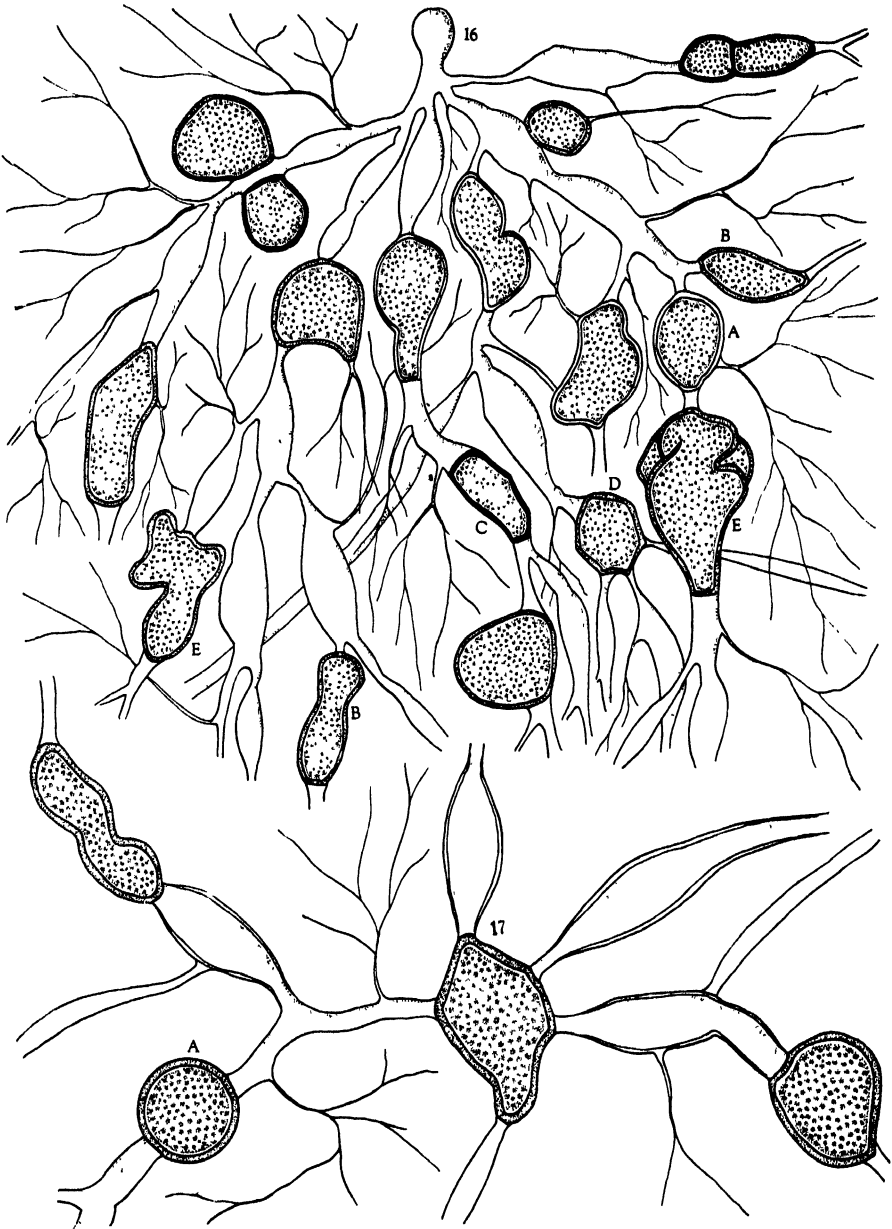
FIGS. 1-15. *Nowakowskiella crassa*. FIG. 1. Portion of vegetative rhizomycelium showing variations in size and shape of intercalary swellings and habit of branching,  $\times 800$ . FIG. 2. Dehiscence of sporangium,  $\times 800$ . FIG. 3. Zoospores in motile phase,  $\times 1450$ . FIG. 4. Creeping, amoeboid zoospores,  $\times 1450$ . FIGS. 5-10. Successive maturation stages in fully-formed and variously-shaped sporangia,  $\times 800$ . FIG. 11. Early developmental stage of intercalary resting spore,  $\times 800$ . FIGS. 12-15. Variations in size and shape of resting spores,  $\times 800$ .

As shown in figure 1, the outstanding characteristic of this species is its coarse rhizomycelium which usually surpasses in diameter and extent of growth that of *N. profusa* (Karling 1941, 1944), the species of *Nowakowskiella* that it resembles most closely. The thallus of these two species may be fairly similar in size, but they are readily distinguishable by the lack or rare presence of well-defined intercalary swellings in *N. profusa* and their abundance in *N. crassa*. The tenuous portions of the rhizomycelium and intercalary enlargements of the latter species may be up to  $18\mu$  and  $25\mu$  in diameter respectively, and in this respect it resembles the coarser species of *Septochytrium* also (Berdan 1942; Karling 1942; Johanson 1943). However, its rhizomycelium lacks the pseudo-septa or trabeculae which are reported to be characteristic of *Septochytrium*. As it grows away from the substratum into the surrounding water, the rhizomycelium may frequently turn and coil, and form an intricate, dense mass of twisted filaments as in *S. macrosporum* (Karling 1945).

The so-called spindle organs or intercalary swellings are very abundant and vary markedly in size and shape. They are predominately oval, ellipsoidal and broadly spindle-shaped, but frequently they may be almost spherical or quite irregular, particularly when they occur at the junction of several branches (figs. 1A, 1B, 1C). So far they have never been found to be septate nor delimited from the remainder of the rhizomycelium by septa except when they give rise to sporangia or resting spores. In the young and rapidly growing portions of the thalli they usually contain a large number of refractive granules which are aggregated in the center (figs. 1D, 1E, 1F, 1G), but in the older parts they become progressively more vacuolate (figs. 1H, 1I, 1J) and often appear to be empty.

As in other species of *Nowakowskiella*, the rhizoids are very abundant in *N. crassa*. They may arise from the tenuous filaments (fig. 1) as well as from the intercalary swellings and sporangia which have originated from intercalary enlargements. For a species with such a coarse and large rhizomycelium, the majority of the sporangia are comparatively small, although large ones may occur occasionally. They are predominately subspherical (figs. 2, 10) and pyriform (fig. 7), but fusiform, obclavate, elongate (fig. 5), and irregular ones occur fairly often. The exit papilla is usually broad and prominent with a relatively large hyaline zone underneath (figs. 5-9). Occasionally two papillae may be found on large irregular sporangia, but as a rule they occur singly. The operculum is pushed up and to one side as the zoospores emerge (fig. 2) and remains attached for several hours after dehiscence.

The zoospores of this species are comparatively small, and as in *N. profusa* and *N. delica* (Whiffen 1943) their hyaline refractive globule is



FIGS. 16, 17. *Polychytrium aggregatum* (?). FIG. 16. Portion of a thallus on chitin showing the abundance, size, shape, content and color of the resting spores,  $\times 800$ . FIG. 17. Enlarged portion of the thallus showing thickening of the walls of the intercalary enlargements,  $\times 1100$ .



quite small (figs. 3-4). The discharge of the zoospores, their initial behavior after emerging (figs. 3, 4), and method of swimming are fundamentally similar to those of other species of *Nowakowskiella*. As the zoospores come to rest the nuclear cap is usually clearly visible and stands out rather sharply as a lunate body (figs. 3, 4).

The resting spores of *N. crassa* may be intercalary or terminal, although the majority observed to date were intercalary. They usually develop from the intercalary enlargements (figs. 11-15) and are comparatively small and predominantly oval or ellipsoidal in shape (figs. 11, 12, 15) with coarsely but evenly granular content, and a smooth hyaline wall. Thus, in structure and general appearance they are similar to those of *N. profusa*, with the exception of their hyaline color.

Except for the specific structural and morphological characteristics noted above, *N. crassa* is fundamentally like other species of this genus. Germination of the zoospores, development of the thallus, formation and maturation of the sporangia (figs. 5-10), and the development of the resting spores are essentially the same and need not be described in detail.

**Cladochytrium aureum** Karling, sp. nov. Fungus saprophyticus. Rhizomycelio exili et angusto, partibus tenuibus  $1.2-3.5\mu$  diam., amplificationibus intercalaribus septatis, ovalibus,  $6-8 \times 9-12\mu$ , fusiformibus,  $5-8 \times 10-17\mu$ , aut irregularibus. Sporangiiis terminalibus aut intercalaribus, ovalibus, aut citriformibus,  $8-19 \times 10-23\mu$ , aut subsphaericis,  $8-36\mu$ . Zoosporis sphaericis,  $5.8-6.2\mu$ , uno globulo luteo-rufo refractivo conspicuo,  $2-2.4\mu$  diam.; flagello  $27-29\mu$  longo. Sporis perdurantibus levibus, sphaericis,  $9-17\mu$ , aut ovalibus,  $8-12 \times 11-16\mu$ , aut fusiformibus; germinatione ignota.

Saprophytic in dead and disintegrating vegetable debris in soil and water, route 234, Charles County, Maryland.

As noted earlier this species is almost identical to *C. tenue* except for its larger zoospores and the presence of a brilliant golden-orange or red body in them. Except for these differences the drawings of *C. tenue* (Karling 1945, figs. 31-45) serve very well as illustrations for this species also, and for this reason the author does not believe additional illustrations are essential to an adequate description of *C. aureum*. Its delicate rhizomycelium, septate, bicellular to multicellular spindle organs, and zoospores are also very similar to those of *C. replicatum* (Karling 1931), but so far no sporangia with exit tubes or spiny spores like those of *C. replicatum* have been found in the Maryland species. In color and size it also resembles to some degree the doubtful and incompletely known *C. polystomum* which Zopf (1884) illustrated but did not describe. However, in this species the sporangia bear several long exit tubes, which apparently are lacking in *C. aureum*. The other fully known species of *Cladochytrium*, *C. crassum* (Hillebrand 1941) and *C. hyalinum* (Berdan 1941) are hyaline, markedly larger, and quite distinct from the present species.

**Additional Polycentric Chytrids.** In addition to the two new species described above several other polycentric chytrids were isolated from water and soil containing animal and vegetable debris from various parts of Maryland. These include *Catenomyces persicinus* (Hanson 1945), Wicomico River, route 234, Charles County and route 236, St. Mary's County; *Cladochytrium replicatum*, route 505, Calvert County, Centerville, Queen Anne's County, Monocacy River at Route 40, Frederick County and Fish Hatchery on Severn Run, Anne Arundel County, and route 234, Charles County; *C. hyalinum*, Old Spout Farm, Calvert County, Centerville, Queen Anne's County, and Savage River, Garrett County; *C. tenue*, route 504, Calvert County and route 234, Charles County; *Nowakowskiella profusa*, Monocacy River at route 40, Frederick County, route 234, Charles County, and Savage River, Garrett County; *N. macrospora*, route 234, Charles County and route 505, Calvert County; *N. elegans*, route 300 between Sluderville and Church Hill, Queen Anne's County, Stonsifer's farm, Frederick County, route 509, Calvert County, Fish Hatchery on Severn Run, Anne Arundel County, and route 234, Charles County; *N. hemisphaerospora* (Shanor 1942) Fish Hatchery on Severn Run, Anne Arundel County, route 234, Charles County, Monocacy River at Miller's Bridge, Frederick County, routes 509 and 505, Calvert County, and route 300, Queen Anne's County; *N. granulata*, route 504, Calvert County; *Septochytrium variabile*, route 503 to Drum point Beach, Calvert County; *Mycelochytrium fulgens* (Johanson 1945), Monocacy River at Miller's Bridge and Keesville, Frederick County, Wicomico River and route 234, Charles County, and route 300 near Sluderville, Queen Anne's County; *Polychytrium aggregatum* on routes 503 and 504, Calvert County.

In relation to *P. aggregatum* it may be noted that thick-walled, brown cysts or resting spores were found in one culture which was isolated on chitin from wet soil collected besides route 504 near Dowell, Calvert County. Inasmuch as resting spores have never been found in *Polychytrium*, this discovery is significant in extending our knowledge of the life cycle of this genus. However, only resting spores, and no sporangia or zoospores were formed in this culture. Conversely, other typical cultures of *P. aggregatum* formed only sporangia and zoospores. Therefore, it is not certain whether the Dowell culture relates to *P. aggregatum* or to a new species of this genus. Nevertheless, as shown in figure 16, its thallus is strikingly similar to that of *P. aggregatum* in appearance, development, organization, and structure.

The resting spores begin as hyaline, relatively thin-walled, enlargements or lateral outgrowths of the rhizomycelium in which the dense, finely granular protoplasm accumulates. As they increase in size they are delimited from the remainder of the thallus by cross septa and gradually become thick-walled and brown in color. It is not certain, however, that this color is a

specific characteristic because the whole rhizomycelium may take on the color of the surrounding water and turn brown with age. The intercalary enlargements and tenuous portions of the rhizomycelium may also become thick-walled, as shown in figure 17. The mature resting spores vary markedly in size and shape, as shown in figure 16. They may be almost spherical (fig. 17A), oval,  $10-24 \times 14-30\mu$  (fig. 16A), oblong,  $12-16 \times 22-34\mu$ , elongate,  $9-12 \times 22-38\mu$  (fig. 16B), truncate (fig. 16C), angular (fig. 16D), deeply lobed (fig. 16E), or very irregular. Although several empty spores have been found, it is not yet known whether they give rise directly to zoospores or function as prosperangia in germination.

No evidence of sexuality has been observed in relation to their formation and development, and in this respect *Polychytrium* appears to be very similar to the other genera of the Cladochytriaceae. However, it is not yet certain that it belongs in this family. The fact that no evidence of sexuality has been found does not preclude the possibility that the thallus on which the resting spores are formed may have arisen from a zygote, or that the resting spores may give rise to gametes in germination as in *Catenaria* (Couch 1945) and other members of the Blastocladales. Therefore, until these details of its life cycle are known the taxonomic position of *Polychytrium* will remain doubtful.

#### SUMMARY

In a survey of the soil fungi of Maryland two new polycentric chytrids were collected and isolated on cellulosic substrata. The first of these species is characterized primarily by an unusually large coarse rhizomycelium which lacks pseudo-septa or trabeculae, and by operculate sporangia. Accordingly, it belongs in the genus *Nowakowskiella* and is described as a new species, *N. crassa*. The second species belongs in *Cladochytrium* and is distinguished by a very delicate rhizomycelium, bi- to multiseptate spindle organs, inoperculate sporangia and large zoospores which contain a brilliant, golden-orange or red refractive body. It is very similar to *C. tenue* except for its pigmentation and larger zoospores, and because of these characteristic differences it is diagnosed as a new species and named *C. aureum*.

In addition to these species several other saprophytic polycentric chytrids were isolated from soil and water in various parts of Maryland. These include: *Cladochytrium tenue*, *C. replicatum*, *C. hyalinum*, *Nowakowskiella elegans*, *N. profusa*, *N. macrospora*, *N. hemisphaerospora*, *N. granulata*, *Septochytrium variabile*, *Catenomyces persicinus*, *Myceliochytrium fulgens*, and *Polychytrium aggregatum*. Resting spores were discovered for the first time in *Polychytrium*.

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## TORREYA

**Vernacular Names for *Roccella*. An Etymological Note.** During the editing of an article by William F. Leggett on "Lichens as Dye Plants" for the Journal of the New York Botanical Garden, where it appeared in May 1949, my attention was drawn so many times to the various designations for the dye-yielding lichens and to their origin, spelling, and even pronunciation (for who can edit a paper without forming the sound of the words in his mind?), that I began to investigate the vernacular names used in different languages for *Roccella*. This, the generic name for the principal dye lichen, *R. tinctoria*, also is one of the names for the plant in Italian, and a word which in turn provided the surname for a famous Florentine family whose wealth was based on its monopoly in the 13th century of the lichen dye industry.

*Roccella tinctoria* was apparently known as a source of red and purple dye in the Holy Land many hundred years before the time of Christ. Its use in the eastern Mediterranean was the subject of comment by the early naturalists. In the Middle Ages it became known in Italy; later the lichen was discovered in the Canaries and on the west coast of Africa. It is only in fairly recent years that it has been completely supplanted by chemically made dyes—except for the manufacture of litmus paper, for which it still is used.

In English this lichen, and also the dye that it gives, are both generally called "orchil" or "archil."

The origin of the word *orchil* seems to be a matter of conjecture and dispute, even among such authorities as the "Oxford"<sup>1</sup> and "Webster."<sup>2</sup> The spelling and pronunciation of the word are also far from stable. In Webster, *archil* is given as the preferred form, with *orchil*, *orchal*, and *orchilla* as variants, all with a *k* sound except under the separate entry for *orchil*, where the English *ch* sound is given as second choice.

In the Oxford, on the other hand, the principal entry is *orchil*, given only with the *ch* sound, but with a cross-reference to *archil*, called a corruption of *orchil*, and pronounced with either a *ch* or a *k* sound (the *k* second choice). The date on which both words first occurred in the English language is given as 1483, *orchil* being used by Shakespeare for the dye in Act I of "Richard II"; *archil* referring essentially to the plant in "Richard III."

<sup>1</sup> *The Oxford English Dictionary*. 1933.

<sup>2</sup> *Webster's New International Dictionary of the English Language*. Second edition, unabridged, 1935.

One wonders whether these distinctions, made in a day when the language was in its incipient stages, were actual or unintentional. *Orchil* for the plant was first recorded in 1758 in the Philosophical Transactions of the Royal Society of London. *Orchilla* or *orchella* (with *ch* sound), meaning the same things, did not appear until 1772, according to the Oxford.

It seems curious that a word which was in use in Shakespeare's day should be designated "origin uncertain" in the Oxford and other comprehensive dictionaries.

The Webster unabridged dictionary seems to go far afield when it states, under *archil*, "Perhaps from Latin *herba urceolaris*, a plant used for polishing glass pitchers." But *herba urceolaris* is given in Riddell's Latin-English lexicon as "pellitory-of-the-wall" (*Parietaria officinalis*) of the nettle family (not the common pellitory, which is a small composite resembling chamomile). So far, no reference has been found to suggest that either the flowering plant *Parietaria* or any lichen in the world has ever been used for polishing.

The botanical name of *Roccella* is more closely allied to *orchil* and to the modern French form *orseille*,<sup>3</sup> which is commonly used among dyers in this country today, than at first seems evident. It is a custom of language occasionally to invert an R and a vowel. (It occurred in English in the word "ran," which was originally "arn.") In the Italian vernacular, according to Pietro Antonio Micheli, the great 18th century mycologist, in his "Nova Plantarum Generum" (1729), the lichen used for dyeing was called *roccella*, *orcella*, or *raspa*,<sup>4</sup> and the dye itself was known as *oricella*. The *ch* sound of the Italian *c* when followed by an *e* as in these words, gives good ground for the Oxford preference for the soft *ch* in *orchil*, *orchilla*, and *orchella*—and also gives a logical source for the English name of the plant, however varied it may be. This is a type of word which would enter a language through the speech of workers, rather than through literature. It is therefore the pronunciation rather than the spelling that would be carried over.

The common name of the lichen in Italy goes back long before the date of Micheli, and even before the "Italian Natural History of 1599" mentioned in *A Modern Herbal* by Grieve and Leyel (1931).

An American vice-consul in Florence once asked that a privately printed book which he had seen in Italy be presented to the Astor Library (now part of the New York Public Library). This was a history of the

<sup>3</sup> An earlier French form was *lorchel*, according to Littré, *Dictionnaire de la Langue Française*. *Orseille* is pronounced *or-sale* in both languages, according to Larousse and Littré in French, and Webster in English.

<sup>4</sup> *Respa* and *rusca* are mentioned in other Italian sources, but neither these nor *raspa* seems to have survived.

famous Rucellai family of Florence,<sup>5</sup> and it is one of the few places where the origin of the family name and its connection with the lichen used for dyeing are recounted.

"And our ancestors were lichen dyers," says the author, "and in that period there was no one in Florence nor even in all Italy except these ancestors of ours who knew how to dye with lichens." One of them had gone to the Levant, where the art had been known from the earliest days, and brought the secret of the process back with him. "And this was the cause which gave so much wealth and good living to our family . . . and from this art of the lichen dye is derived the name of Rucellai" (italic mine). The name was originally Oricellai (it occurred also in various other spellings), but it is as Rucellai that the family became famous.

The name first achieved prominence about 1250, but it was previous to that time that one Marco di Giunta d'Alamanno di Monte de messer Ferro came to Italy in the retinue of an emperor (possibly Frederick II, grandson of Frederick Barbarossa, who was crowned in Rome in 1220). The stories say he came from Brittany, but from his name one might judge that he had come from Germany (then called Allemania). He settled in Florence and established a successful mercantile business there, dealing in woollens and carrying on commerce with distant places. One of his family, probably Federigo, spent a long time in the islands of the eastern Mediterranean, where he found a native lichen being used as a purple dye. This was obviously the plant which both Theophrastus and Pliny had recorded as growing in rocks along the seashore of Crete, and used for producing a beautiful purple dye on woollens. They both gave the common name of "seaweed" to it, and Pliny noted that no language had any other name for it than that used by the Greeks, *Phycos thalassion*.

So the date when the names of *roccella* and *orcella* came into the language that Dante crystalized is obscured in those first twelve centuries of the Christian era. The Spanish, at some time during that period, adopted the name of *orciglia*, or *orciglio*, and also used *orchilla* and *orchillo*, and the Portuguese said *urzela* (or *urzella*), all obviously related to the Italian word for the lichen and its dye.

Some of the early botanical authors say that the present generic name for the lichen, *Roccella*, is a diminutive formed from *rocca*, because the species always grows on rocks (botany is full of such "made up" derivations). But this does not seem probable, since the word *rocca* does not appear in the classical Latin from which botanical names are most often derived. It is possible that the Italian vernacular name of *roccella* or *orcella* had this derivation, but the Oxford dictionary dismisses all such

<sup>5</sup> "Un mercante fiorentino, Giovanni Rucellai, e la sua famiglia nel secolo XV" by G. Marcotti, published in Florence in 1881.

claims with the flat statement: "Whether the original was *Oricello* or *Or-ciglio*, a derivation from *rocca*, rock, founded on modern Latin *roccella*, is out of the question."

Five hundred years after the Rucellai family was established and named for the dye-producing lichen which brought it wealth, Linnaeus, following some of his botanical predecessors, called the plant *Lichen Roc-cella* in his *Species Plantarum* (ed. 2. 1763). In 1805 Augustin Pyramus de Candolle adopted the name *Roccella tinctoria* for the plant, and this it has remained to the present day.

The name *Lacca musica* also occurs for *Roccella tinctoria* in reference books, but it seems to have no significance, except as a pseudo-Latin form in which *musica* is an oft-repeated error for *musci*. Or, it may be an extension of the two syllables of *lacmus*, which is another name for *litmus*, a coloring substance also derived from this lichen.

These two words pose a similar problem, for if we follow the Webster unabridged dictionary, the *-mus* in *litmus* stems from the Old Norse word for moss, added to *litr*, meaning dye or color. Thus it was recognized early as a dye plant. But the *-mus* in *lacmus* comes from the Dutch *moes*, meaning pulp; the *lac* comes from *lak*, meaning stain, in the original Dutch word.<sup>6</sup> *Lacmus*, therefore, if the difference actually exists, first referred to the dye itself, whereas *litmus*, now seldom thought of except as a changeable coloring matter used for testing acidity and alkalinity, in its original form referred only to the lichen from which the dye was obtained.—CAROL H. WOODWARD.

**A Note on Buried Cedar Logs at Secaucus, N. J.** In the Hackensack tidal marsh at Secaucus, N. J., a great number of logs of southern white cedar [*Chamaecyparis thyoides* (L.) B.S.P.] were recently excavated by the New Jersey State Highway Department. During the winter of 1947-1948, the Highway Department, in preparation for building a new road, removed great quantities of cedar peat for almost a quarter of a mile on the northeast side of Secaucus. It was the purpose of the excavation to remove the peat down to the clay bottom, at an average depth of ten feet, in order to obtain a sound base for fill material. In the course of the operation, many cedar logs were removed and are now strewn with the peat along the new highway.

Many of these logs are large and well preserved. The largest specimen is shown in figure 1. This tree was three feet d.b.h. when it ceased growing. Unfortunately it had its bole broken at about twenty feet. Its bark is well in place to about ten feet above the base and preserved so that it appears as if the tree had fallen only a short time ago. The bark is not charred, indicating that the tree had not been subjected to any severe burning. Ring counts were made at approximately six feet from the base. This was done by cutting out a section with an axe and smoothing a face with a mallet and

<sup>6</sup> The Oxford, however, says that *litmus*, which came into the language in 1502, is altered from the Old Dutch word that in 1794 gave us *lacmus*, and while referring to the Old Norwegian *litmosi*, does not observe the difference in original meaning. A Norwegian encyclopedia indicates "dye moss" for both derivation and present meaning of the word, and refers to the Old Norse form, *litmosi*. Sigrid Undset mentions the "lit-mose" as a dye plant in her first volume of "Kristin Lavransdatter."





chisel. There are 304 rings, making the age of the tree at the time of its death 304 years plus the number of years it took for the tree to reach a height of six feet. Kors-  
tian and Brush<sup>1</sup> found, from growth studies on white cedar in New Jersey, that under  
present climatic conditions seven years are required for a tree to grow to six feet. From  
this information, it then appears that the specimen attained the age of 311 years.

These logs buried below mean sea level at Secaucus are not unusual. Cook noted the  
occurrence of such logs buried below sea level from Nova Scotia to Georgia as early  
as 1857.<sup>2</sup> Since this time reports of similarly buried logs have been frequent. With  
periods of rapid encroachment of the land by the sea, due to land subsidence or rise  
in sea level or both, the salt-intolerant cedar gradually dies and becomes incorporated  
with the peat beneath the surface of the coastal marshes.—C. J. HEUSSEER.

#### REVIEW

**The Study of Plant Communities.** By Henry J. Oosting. 389 pp.  
190 figures. 11 tables. W. H. Freeman & Company, San Francisco, Cali-  
fornia, 1948.

A good basis for an understanding of general plant ecology is provided in this  
book. It can be readily understood by the beginning student; yet it is complete enough  
for a year's course in ecology. The illustrations are well-selected, abundant, but not  
always printed clearly.

In addition to the introduction, sections on the community, environment, com-

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<sup>1</sup> Kors-  
tian, C. F. & Brush, W. D. 1931. Southern white cedar. U. S. Dep. Agr. Tech.  
Bull. 251.

<sup>2</sup> Cook, G. H. 1857. On a subsidence of the land on the sea coast of New Jersey and  
Long Island. Am. Jour. Sci. 74: 341-354.

munity dynamics and practical aspects are included. In each section the material is well-organized and logically presented. The works of some foreign ecologists as well as those published in North America are surveyed, analyzed, and critically evaluated. The short lists of general references at the ends of chapters, in addition to the extensive bibliography preceding the index, are very useful.

*Conopholis americana* unfortunately is listed as a saprophyte (p. 27), but it represents one of the few and minor errors.

The last section, "Practical Considerations," should prove interesting to the lay reader. The importance of ecology in the conservation of renewable natural resources and in the affairs of man generally is clearly indicated. Because of this section, it should prove to be an unusually valuable biological textbook.—A. J. SHARP.

#### PROCEEDINGS OF THE CLUB

**Minutes of the Meeting of December 7, 1948.** The meeting was called to order by President Small at 8:05 P.M. at Columbia University; 90 members and friends were present. Dr. B. M. Duggar of the Lederle Laboratories spoke on "The Mycological Background of Aureomycin."

The meeting was adjourned at 9:50; no business was transacted.

Respectfully submitted,

DONALD P. ROGERS,

*Recording Secretary.*

# INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

## TAXONOMY, PHYLOGENY AND FLORISTICS

### ALGAE

- Bold, Harold C.** The morphology of *Chlamydomonas chlamydogama* sp. nov.  
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- Thompson, R. H.** Immobile Dinophyceae. 1. New records and a new species. Am.  
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- Baxter, Dow V.** Some resupinate polypores from the region of the Great Lakes.  
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- Bessey, Ernst A.** Studies on *Pilobolus*: *P. Kleinii* and *P. longipes*. Pap. Mich.  
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- Cantino, Edward C.** The physiology of the aquatic Phycomycete, *Blastocladia*  
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\* (See also under Morphology: Wylie, D. E.)

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## DIFFERENTIAL CHROMOSOME SEGMENTS IN *TRILLIUM ERECTUM* L.<sup>1</sup>

PAUL C. BAILEY

In recent years there have appeared numerous papers in the field of cytotaxonomy which have been concerned with the cytological aspects of certain species of *Trillium*. A number of papers have attempted to establish differences between closely related species on the basis of visible differences in their chromosome morphology, the usual criteria of difference being the total length of the chromosomes and the relative length of the chromosome arms.

Haga (1934) concluded from his studies of *Trillium kamstchaticum*, *Trillium smallii* and *Trillium tschonoskii* that, "it is hardly tenable to consider the slight differences in length and form per cents in absolute lengths of the chromosomes found between different species as being significant". Barksdale (1938), as a result of his studies of the pedicellate species of *Trillium* from the southern Appalachians, states "that such an attitude, which seems to result from the assumption that such minor floral and vegetative variations peculiar to any one species will be reflected in the morphology of one or several of the chromosomes of the species complement, is, at least, in the case of *Trillium*, a rather naive one."

If one accepts the conclusions of Haga (1934) and Barksdale (1938), it is then necessary to employ other criteria in order to find cytological differences which may exist between closely related species of the same group.

From time to time there have appeared in the literature accounts of experimental treatment that rendered visible linear differentiations in the chromosomes not otherwise observable. Shmargon (1938) observed these regions in *Secale cereale*, Darlington and LaCour (1938, 1940) in *Paris* and *Trillium* species, Wilson and Boothroyd (1941, 1944) in *Trillium* species and *Secale cereale* and Kakhidze (1938) in *Crepis capillaris*. In animals they have been found by Callan (1924) in *Triton* species. These differentiations have taken the form of regions of reduced diameter and staining capacity, sometimes so numerous as to give the chromosomes a chromomeric appearance. The differentiated regions may be of varying length, and may appear within or at the end of the chromosome arms.

<sup>1</sup> Portion of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Vanderbilt University, Nashville, Tennessee.

The investigations summarized above indicate that such differentiated regions were produced in the somatic chromosomes of a variety of plants. Darlington and LaCour (1938, 1940) produced regions of reduced diameter, highly specific as to locality, in mitotic metaphase and anaphase chromosomes of *Paris* and *Trillium* by cold treatment for several days; they called this phenomenon "differential reactivity." This term, as used by Darlington and LaCour (1938, 1940), describes a condition entirely similar to the regions of reduced diameter and staining capacity reported by the other cited investigators. The same effect was obtained by Kagawa (1929) and Ellenhorn (1935) by treatment of *Triticum* root tips with chloral hydrate.

In Arctic species of several of the grasses Flovik (1936) found an exceptionally high number of secondary constrictions in most individuals he investigated. In some cases these were so numerous that the chromosomes had a beaded appearance. It appears to the writer that the effective agent in this case may possibly be the constant low temperature in such an environment.

Although experimental proof is not yet available, all the phenomena described above may probably be considered as differential reactivity of chromosomes. Inasmuch as such differential reactivity almost certainly indicates a basic and inherent differential pattern in the chromosomes, knowledge concerning the origin and behavior of such regions is of considerable importance in the understanding of chromosome structure and behavior.

There are many aspects from which differential reactivity might be investigated, chemical methods being especially desirable. Before the latter are undertaken, however, a purely cytological investigation is indicated. Such an approach has been made both by Darlington and LaCour (1938, 1940) and by Wilson and Boothroyd (1941, 1944).

As described by Darlington and LaCour (1940) exposure to cold for a sufficient length of time prevents certain regions of the metaphase and anaphase chromosomes of *Trillium* from staining normally. As a rule these regions were understained, and measured only about one half the diameter of the unaffected portions of the chromosome. Rare exceptions to this were observed in some regions understained but not of reduced diameter, as well as narrower regions which were not understained. The length of constrictions varied, the terminal ones being somewhat longer. Most constrictions occurred in the proximal third of the chromosome arm, but in one chromosome constrictions occurred in the distal third.

According to these same investigators, although the size of the differential segment is subject to some variation, its position is constant and

specific. Each chromosome has a characteristic pattern of differential reactivity, some regions being apparently more readily affected than others, especially the terminal ones.

Wilson and Boothroyd (1941) also devoted attention to the rate with which differential segments appeared. They exposed root tips of *Trillium erectum* L. to 3° C. for periods of from 15 minutes to four weeks. Differential regions appeared after 30 minutes, and after exposure for 96 hours nearly all chromosomes were affected. These investigators concluded that in *Trillium erectum* L. maximum differential reactivity had been reached by 96 hours of cold treatment. Although they considered their work on recovery rate somewhat inadequate, they found the time for recovery to be much shorter than that required for the differential segments to appear. After 90 hours exposure to cold the chromosomes returned to normal in about 10 hours at room temperature, most of the recovery occurring in 4 or 5 hours. The relatively rapid rate of recovery is not unexpected, however, inasmuch as the rate of mitosis must also be increased at room temperature.

Darlington and LaCour (1940) believe that differentiated segments produced by cold are the results of nucleic acid starvation. They state that, "... in *Trillium*, nucleic acid starvation requires three days to affect the metaphase of mitosis in the roots. Even at a low temperature this period must comprise most of the resting stage. The starvation effect therefore acts long before the prophase when the chromosomes are actually taking up nucleic acid." This is in sharp contrast to the observations of Wilson and Boothroyd who observed the beginnings of differentiation after only half an hour at 3° C. Darlington and LaCour (1940) also state that the differentiated segments represent the heterochromatic regions of the chromosomes, and identify them with the chromocenters of the resting nucleus.

Wilson and Boothroyd (1944) are of the opinion, "that the differential staining capacity of the various parts of the chromosomes under the stimulus of cold is essentially due to a difference in their contraction, which is a manifestation of differential coiling." This they say, "may or may not be causally related to an upset in the nucleic acid metabolism."

Darlington and LaCour (1940) have illustrated a number of homologous pairs of chromosomes that differ in number, size, or position of the differential segments, or in various combinations of these. They designated such pairs as hybrids, but Wilson and Boothroyd (1944) prefer to call them heterogeneous pairs because the term implies genetic hybridity. They also point out that even this assumption may not be justified, inasmuch as one cannot be certain that differential reactivity has not reached



a point of stability, and even when this is reached, it is not clear how long stability lasts.

With regard to the length of the cold-treated chromosomes Darlington and LaCour (1940) report that, "certain segments in each chromosome are reduced to half the standard diameter of the chromatid and appear understained from late prophase until anaphase. They remain their usual length." They also state that, "the heterochromatic segments are the same length when under-charged as when normally charged." The term "charged" as used by Darlington and LaCour (1940) here refers to the charging and under-charging of the chromosomes with nucleic acid.

Wilson and Boothroyd (1944) have observed differentiations of the chromosomes from late prophase until telophase, "during which time their contraction is greatest." With regard to the length of the chromosomes during cold treatment they observe that, "low temperatures cause greater than normal mitotic contraction of the chromosomes" and that, "there is clear evidence of related differential reactions of chromosome segments in both stainability and contraction following a period of cold treatment." These investigators measured the length of the normal chromosome complement as well as that following cold treatment. They found that the total length of the chromosome set ( $2n$ ) was reduced from  $285 \pm 6.9$  microns, the length of the normal complement, to  $234 \pm 4.5$  microns after 96 hours at  $3^{\circ}$  C.

Darlington and LaCour (1940) suggest that differential reactivity may be used as a genetic and taxonomic indicator, a criterion of variation between species. It was the primary purpose of the present study to determine whether there exists any such variation between the Canadian *Trillium erectum* L. studied by Wilson and Boothroyd (1941, 1944) and the same species as found in the southeastern United States. If differential reactivity is a constant, specifically recurring phenomenon, the Canadian and Tennessee plants of *Trillium erectum* L. should exhibit the same pattern in response to low temperature treatment.

**Material and Methods.** A total of approximately 300 rhizomes of *Trillium erectum* L. were collected at the foot of the Cumberland escarpment near Sparta, Tennessee. Some were planted in a bed out-of-doors and others were potted in the greenhouse. An abundance of fresh growing tips was available almost continually. Cold treatment was provided with a commercial electric refrigerator which maintained a fairly constant cold temperature at  $3^{\circ}$  C. The cold-treated root tips were secured from rhizomes which had been placed in peat moss before transfer to the refrigerator.

Most material for study was prepared using the Feulgen technique together with a squash method. A detailed account of the procedure is sum-

TABLE 1. Comparative data on chromosome morphology of *T. erectum* L. and *T. luteum* (Muhl.) Harbison

Material	Chromosome A			Chromosome B			Chromosome C			Chromosome D			Chromosome E			Total
	L.A.	S.A.	T.L.	L.A.	S.A.	T.L.	L.A.	S.A.	T.L.	L.A.	S.A.	T.L.	L.A.	S.A.	T.L.	Length
1. <i>T. erectum</i> Feulgen Tech.	15.6	1.7	17.3	15.0	4.7	19.7	9.3	5.1	16.4	12.3	8.3	20.6	14.2	13.5	27.7	199.4
2. <i>T. erectum</i> Feulgen Tech.	16.1	1.1	17.2	13.0	5.9	18.9	8.7	5.4	14.1	9.9	6.3	15.2	14.1	12.7	26.8	186.4
3. <i>T. erectum</i> Aceto-carn.			22.3	20.7	8.4	29.1	12.2	9.5	21.7	16.1	12.2	28.3	20.1	20.1	40.2	285.0 ± 6.9
4. <i>T. erectum</i> Aceto-carn.			18.7	16.4	8.5	24.9	9.4	9.4	18.8	13.0	10.0	23.0	15.8	15.8	31.6	234.0 ± 4.5
5. <i>T. erectum</i> Aceto-carn.	20.2	1.5	21.7	16.8	11.7	28.5	10.5	8.5	19.0	14.2	9.1	23.3	20.7	19.8	40.5	266.0
6. <i>T. erectum</i> Aceto-carn.	13.6	1.5	15.1	13.3	7.5	20.8	8.4	6.2	14.6	14.0	7.6	21.6	14.7	13.8	28.5	201.2
7. <i>T. luteum</i> Aceto-carn.	19.8	1.5	21.3	15.3	11.0	26.3	13.3	10.3	23.6	19.1	6.7	25.8	21.0	18.7	39.7	273.4
8. <i>T. luteum</i> Feulgen Tech.	11.2	1.5	12.7	16.1	5.8	21.9	8.7	5.7	14.4	13.3	7.0	20.3	14.4	13.1	27.5	193.6

1. *T. erectum* L., normal, Feulgen technique in present study.

2. *T. erectum* L., 3° C. for 96 hours, Feulgen technique in present study.

3. *T. erectum* L., normal, Aceto-carmin technique in study of Wilson and Boothroyd.

4. *T. erectum* L., 3° C. for 96 hours, Aceto-carmin technique in study of Wilson and Boothroyd.

5. *T. erectum* L., normal, Aceto-carmin technique in present study.

6. *T. erectum* L., 3° C. for 96 hours, Aceto-carmin technique in present study.

7. *T. luteum* (Muhl.) Harbison, normal, Aceto-carmin technique in present study.

8. *T. luteum* (Muhl.) Harbison, normal, Feulgen technique in present study.

L.A.—Long Arm; S.A.—Short Arm; T.L.—Total Length.

Standard deviations for the total lengths of individual chromosomes in this study range from 0.5 to 1.2.

marized by Woodard (1948). The aceto-carminic technique employed by Wilson and Boothroyd (1944) in their study of differential reactivity was also used by the writer for comparative study as discussed in a later section.

#### OBSERVATIONS AND DISCUSSION

**Normal Chromosome Complement.** The morphology of the normal (non-cold treated) chromosome set of *Trillium erectum* L. (fig. 6) was carefully studied. Measurements were made of more than 100 chromosomes of each type (A, B, C, D, and E) in the  $2n$  root tip complement. The results of these measurements are summarized in table I, 1 which shows the total length of the chromosomes as well as the length of the chromosome arms.

A total of 21 different plants was employed in studying the normal chromosome complement. A number of root tips were secured from each and an accurate record maintained of slides made from each plant, in order to determine whether any variations occurred. No variations of any significance were found. Included in the 21 were two plants of the albino strain which also showed no variations in chromosome size.

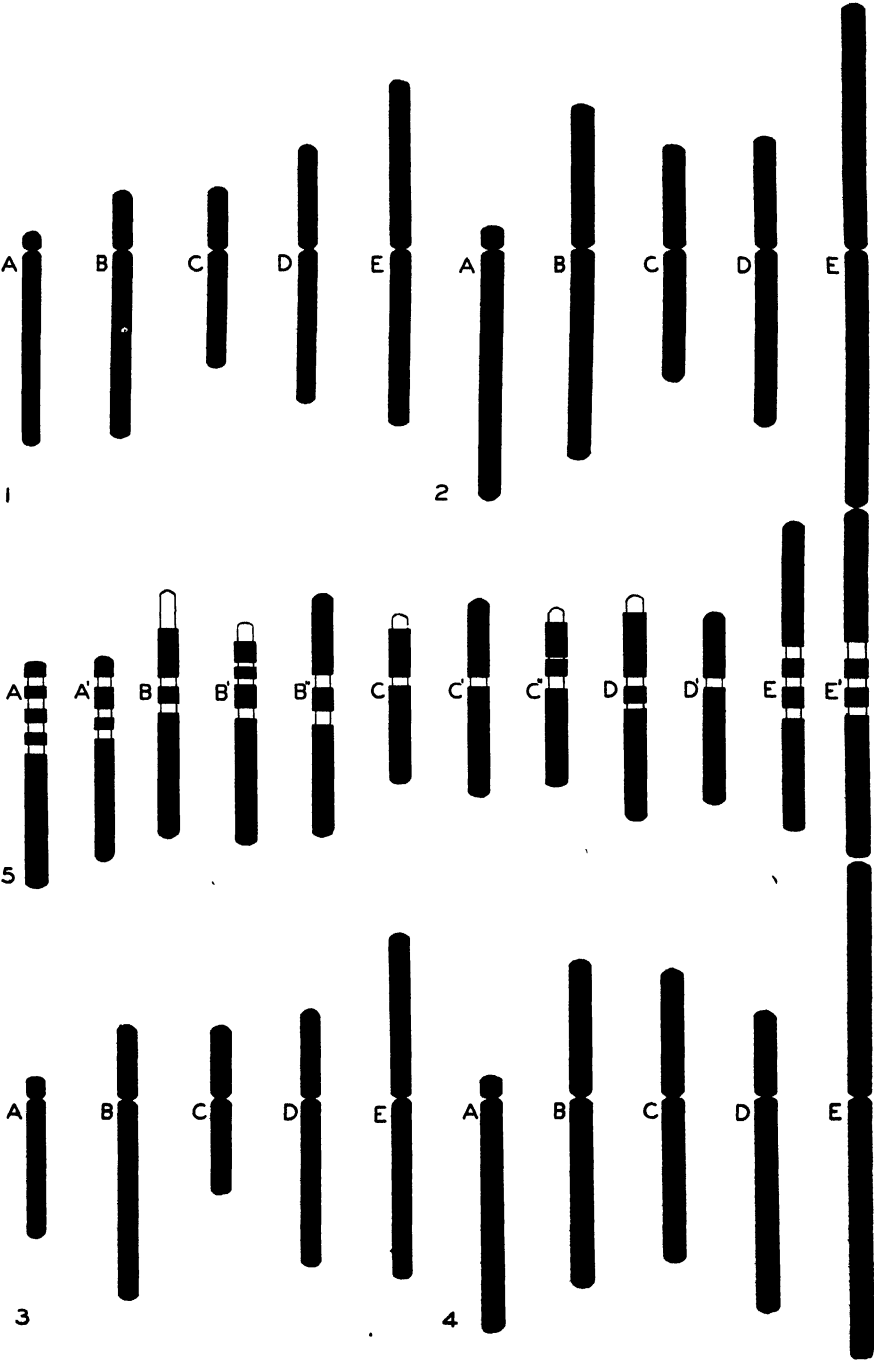
A diagram showing the relative lengths of the chromosome arms is given in figure 1. This reveals that the primary constriction of chromosome A is sub-terminal; those of B, C, and D are sub-medial; and that of chromosome E has an almost medial, actually a sub-medial primary constriction.

The total length of the normal diploid chromosome set was found to be 199.4 microns (table I, 1). This figure is much lower than that found by Wilson and Boothroyd (1944) for their Canadian plants of the same species, their figure for the normal complement being  $285 \pm 6.9$  microns (table I, 3). This difference in the total length of the normal complement, however, can be attributed entirely to the difference in the techniques employed in the two studies as will appear later. Wilson and Boothroyd (1944) used the aceto-carminic technique obtaining the results shown in table I, 3.

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FIGS. 1-5. Diagrammatic analysis of chromosome morphology of *T. erectum* L. and *T. luteum* (Muhl.) Harbison based upon measurements of mitotic metaphase chromosomes. Fig. 1. Normal chromosome complement of *T. erectum* L. prepared by the Feulgen squash technique. Fig. 2. Normal chromosome set of *T. erectum* L. prepared by aceto-carminic technique. Fig. 3. Normal chromosome complement of *T. luteum* (Muhl.) Harbison prepared by the Feulgen squash technique. Fig. 4. Normal chromosome complement of *T. luteum* (Muhl.) Harbison prepared by aceto-carminic technique. Fig. 5. Chromosomes of *T. erectum* L. after  $3^{\circ}$  C. for 96 hours using the Feulgen squash technique. Types of patterns of differentially reactive segments are shown for each individual chromosome after treatment with cold. Marked contraction of these chromosomes is apparent.

All figures are drawn to scale at an approximate magnification of  $\times 1650$  after reduction.



The writer also used the identical technique employed by Wilson and Boothroyd (1944) as a check on root tips of the same species occurring in Tennessee, and obtained a total length of 265 microns (table I, 5). Figures 1 and 2 illustrate comparatively the effect of the two techniques on the chromosomes of the same species of *Trillium*. Figures 6 and 7 are photomicrographs illustrating this difference. The figures clearly indicate that no valid comparison can be made between chromosome lengths unless identical methods of preparation have been employed. There is a difference of 20 microns in the total length of the normal complement between the results obtained by Wilson and Boothroyd (1944) and those obtained by the writer using the same technique (table I, 3 and 5). The figure obtained in this study with the aceto-carmin technique (table I, 5), however, approaches much more closely that of Wilson and Boothroyd (1944) than that obtained using the Feulgen technique (table I, 1). The difference of 20 microns between the results of Wilson and Boothroyd (1944) and those of the writer, using the same technique, is not regarded as significant, inasmuch as measurements of individual chromosomes (table I, 5) are all somewhat lower than those obtained by Wilson and Boothroyd (1944) (table I, 3). This is perhaps occasioned by measuring metaphase chromosomes which had not achieved maximum contraction, a point difficult to ascertain infallibly. Further indications that the method of preparation is highly important in making comparisons will appear later.

Study of the data of Wilson and Boothroyd (1944) reveals in addition that they found the primary constriction to be more median in Chromosomes B, C, D, and E than here reported for the southern plants. Sufficient measurements were not available in their paper to determine whether this was true for chromosome A. From their figures it is possible to obtain ratios of the length of the short arm and the long arm. Such calculations were made in order to compare their results as to the position of the primary constriction with those of the writer. The ratios are given in table II.

The most noticeable discrepancy occurs in comparing the ratios of chromosomes C and D. Wilson and Boothroyd (1944) reported that the primary constriction of chromosome C was actually very slightly more median than in chromosome D; however, the ratios are almost identical even though the absolute length of C is considerably shorter than D. Chromosome C in the writer's material was also found to be much shorter than D, but the difference in the ratios between C and D in the Tennessee material is striking. The primary constrictions of chromosomes C and D were both found to be more sub-median in this study, and that of D was found to be more median than that of C. It can be seen from the ratios (table II)

that the differences between those based on Wilson and Boothroyd's data (1944), especially for chromosome C, and those found in the present study are entirely too great to have resulted from slight inaccuracies in measurements and calculations.

Wilson and Boothroyd (1944) found the two arms of chromosome E to be so nearly the same length that they disregarded the difference. Actually a noticeable difference is present in the writer's preparations: the ratio between the long arm and short arm is 95:100, the actual difference in length being 0.7 micron.

TABLE II. *Short-arm, long-arm, ratios in chromosomes of Trillium erectum L. before and after cold treatment.*

	Material	Chr. A	Chr. B.	Chr. C	Chr. D	Chr. E
1.	<i>T. erectum</i> L. Aceto-carmin	no data	40:100	77:100	76:100	100:100
2.	<i>T. erectum</i> L. Feulgen Tech.	10.6:100	31:100	54:100	67.5:100	95:100
3.	<i>T. erectum</i> L. Aceto-carmin	no data	45:100	100:100	64:100	100:100
4.	<i>T. erectum</i> L. Feulgen Tech.	7:100	52:100	61:100	63:100	90:100

1. *T. erectum* L., normal, aceto-carmin technique in study of Wilson and Boothroyd.

2. *T. erectum* L., normal, Feulgen technique in present study.

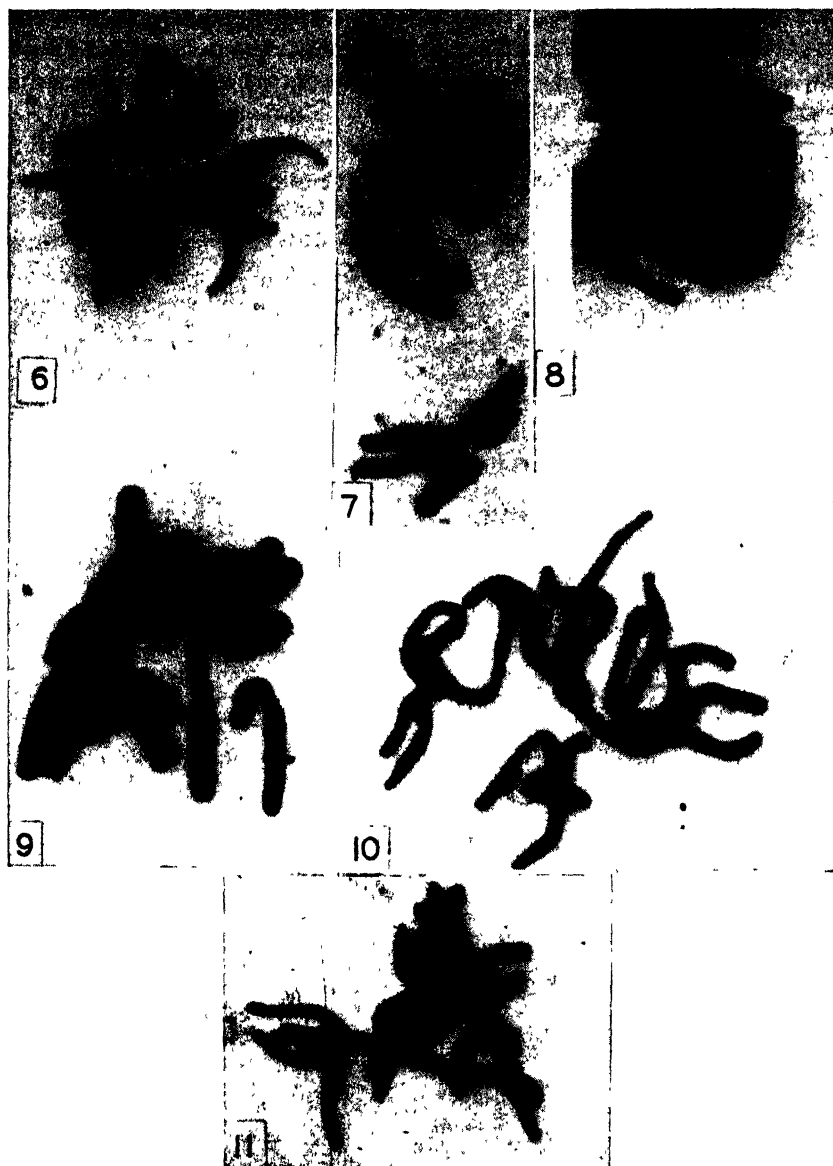
3. *T. erectum* L., 3° C. for 96 hours, aceto-carmin technique in study of Wilson and Boothroyd.

4. *T. erectum* L., 3° C. for 96 hours, Feulgen technique in present study.

No comparison can be made between chromosome A in the material of Wilson and Boothroyd (1944) and of the writer, due to absence of comparative data. It may be noted, however, that the primary constriction of chromosome A is the only sub-terminal one found in the chromosome set.

No secondary constrictions normally occur on any of the chromosomes. The primary constrictions are very prominent, yet very short. The width of all the chromosomes prepared by the same technique is constant, that is, there are no variations in width among the several chromosomes. The average width of the chromosomes using the Feulgen technique is 1.4 microns while it is slightly higher when the aceto-carmin technique is employed, as can be seen in figures 1 and 2 and figures 7 and 9 as compared with figures 6 and 8.

The morphological differences between the chromosome sets summarized in the preceding paragraphs, in the Canadian and Tennessee plants, led the writer to think that the two studies might possibly have been dealing with entirely different plants. Herbarium specimens of Canadian plants



FIGS. 6-11. Photomicrographs of chromosome complements of *T. erectum* L. and *T. luteum* (Muhl.) Harbison. Fig. 6. *T. erectum* L. normal after using the Feulgen technique. Fig. 7. *T. erectum* L. normal after using aceto-carmin technique. Fig. 8. *T. erectum* L. after 3° C. for 96 hours using the Feulgen technique. Fig. 9. *T. erectum* L. after 3° C. for 96 hours using aceto-carmin technique. Fig. 10. *T. luteum* (Muhl.) Harbison normal after using aceto-carmin technique. Fig. 11. *T. luteum* (Muhl.) Harbison normal after using the Feulgen technique.

furnished by Dr. Pierre Dansereau along with plants used in this study were sent to Dr. Wm. A. Anderson of Iowa State University and to Dr. S. J. Smith of Syracuse University for identification. Both identified all plants as *T. erectum* L.

**Differential Pattern.** The position of the differential segments of the chromosomes resulting from cold treatment appeared to be almost constant within the group of plants studied. Figure 5 represents diagrammatically the variation in chromosome complement of *T. erectum* L. after exposure to 3° C. for 96 hours; the position and average size of the differential segments are represented in the diagrams which are drawn to scale. Where more than one chromosome is illustrated for each type, more than one differential pattern appeared in that particular chromosome after treatment.

It is apparent in figure 5 that the differential pattern varies somewhat, and that in chromosomes C and D instances were found where no differential segments appeared after cold treatment. In the case of chromosome C the number of chromosomes in which no differentiation appeared amounted to 10.9% while in chromosome D the number amounted to 28.7%. These percentages are based upon study of more than 100 chromosomes of each type. This apparently indicates that chromosomes A, B, and E are more readily affected by cold treatment than are chromosomes C and D.

It can be seen from the diagrams that not all cold-treated nuclei contain the same number of visibly differentiated segments. The total maximum number of such regions in the diploid nucleus was found to be 24 while in 83.2% of the total number of chromosomes measured only 20 such segments appeared regularly. These results differ markedly from those of Wilson and Boothroyd (1944). They found a total number of 42 differential segments in the diploid nucleus with 24 of the total appearing regularly. Furthermore, in this connection, if each chromosome is considered individually, and if comparisons are made between the Canadian and Tennessee plants, differences are apparent for all plants. Chromosomes A, however, probably shows fewer discrepancies than any of the others. As shown in the diagram three secondary constrictions or differentially reactive segments appeared regularly (fig. 5, A), and in only six chromosomes out of a total of 116 were two secondary constrictions found. Wilson and Boothroyd (1944) also found three secondary constrictions in the same position. They found instances, however, where the differential segments fused making one long differential segment. No examples of this type were observed in the present study. In neither case were differentiated segments found to be distal to the primary constriction.



In chromosome B Wilson and Boothroyd (1944) regularly found one terminal and three interstitial segments. The writer, however, found the terminal and one interstitial constriction to be of regular occurrence (fig. 5, B). In 12 chromosomes out of a total of 100, however, two interstitial segments appeared (fig. 5, B'), one interstitial on either side of the primary constriction. In 11 out of the 100 chromosomes the terminal constriction failed to appear, but the interstitial one in the long arm remained (fig. 5, B''). Wilson and Boothroyd (1944) also found two segments which were not regular in their appearance: one of these occupied the distance between the terminal constriction and an interstitial one. Therefore, when this particular sporadic differential segment appears, the terminal and the closest interstitial one fuse, thus forming one long terminal segment. This might possibly explain the condition in the 12 chromosomes represented by the type B' illustrated in figure 5. Measurements of the relative lengths seem to indicate that this is true. In the regularly recurring pattern, however, Wilson and Boothroyd (1944) found two differential segments more than were observed in the writer's material.

Chromosome C (fig. 5) presents a simpler pattern. Ninety-six chromosomes out of a total of 110 showed only a terminal differential segment (fig. 5, C). Twelve out of the 110 were not affected at all (fig. 5, C'), and two out of the total showed the terminal constriction plus a very short interstitial segment (fig. 5, C''). The latter, one terminal and one interstitial segment, is the pattern found regularly by Wilson and Boothroyd (1944) in chromosome C in their material.

In chromosome D (fig. 5, D) one terminal constriction was found in the short arm and one interstitial or sub-median segment appeared on the the long arm in the writer's preparations. These were the only two differential segments to appear in this chromosome, and both were differentiated regularly. As has already been pointed out, 29 chromosomes out of a total of 109 were not affected by the cold treatment (fig. 5, D'). Wilson and Boothroyd (1944) observed a sub-median constriction and a sub-terminal one on the long arm of chromosome D in addition to the two observed by the writer, thus making a total of four recurring regularly in their plants. They also found another terminal segment which was irregular in its appearance which, when present, was fused with the sub-terminal one.

The differential segments in chromosome E (fig. 5, E) appeared equidistant from the primary constriction. Two sub-median segments occurred, one being in each chromosome arm (fig. 5, E). This was true in 100 chromosomes out of a total of 109. In addition to these two, a smaller sub-median segment appeared in the long arm in nine of the 109 chromosomes (fig. 5, E'). The latter was more terminal than the sub-median segment which ap-

peared regularly. Wilson and Boothroyd (1944) found three corresponding segments in their studies of chromosome E as well as an additional one which was of regular occurrence. The last is similar to the one described by the writer as appearing irregularly (fig. 5, E'), except that it is found on the opposite arm. Both Canadian and Tennessee material thus exhibit one regularly appearing constriction in each arm of chromosome E. Wilson and Boothroyd (1944) also found a terminal and an additional interstitial segment appearing irregularly.

Inasmuch as the two arms of chromosome E are so nearly the same length it is possible to mistake the arm in which the third interstitial segment appears; the irregular appearing constriction might have appeared in either chromosome arm. If this were true, the exception in the present study would correspond to what Wilson and Boothroyd (1944) regard to be the rule.

Homologous chromosomes always presented the same differential pattern regardless of whether it was the regularly or irregularly appearing one. This is significant in that it indicates the pattern is basic and inherent for the chromosomes. However, the fact that the irregularly appearing pattern also is found in both homologous chromosomes is difficult to explain.

In summarizing the comparison between the two studies it is obvious that the behavior of chromosome A upon cold treatment was the same in both Wilson and Boothroyd's (1944) and the writer's observations. What Wilson and Boothroyd's (1944) found to be the rule in chromosomes B, C, and E, this study revealed it be the exception, and in chromosome D no similar patterns were found.

**Contraction.** The study of differentiation was restricted to the mitotic metaphase chromosomes. Measurements of the chromosome complement were made after treatment at 3° C. for 96 hours. Table I shows, in addition to the normal chromosome data referred to in the preceding paragraphs, the length of the individual chromosomes after cold treatment, the total length of the chromosome set, and the length of the long and short arms.

A comparison of the figures in table I reveals the degree of contraction resulting from cold treatment. The total average length of the diploid chromosome set before cold treatment was 199.4 microns (table I, 1) while after 3° C. for 96 hours the total average length was 186.4 microns in Feulgen preparations (table I, 2). Expressed as percentage of contraction this would mean that the chromosomes measured 93.5% of their total length after treatment. Wilson and Boothroyd (1944) found a greater degree of contraction resulting from cold treatment; their measurements (table I, 3)

show the total length to be  $285 \pm 6.9$  microns before treatment and  $234 \pm 4.5$  microns or 82.1% afterwards (table I, 4).

The difference between the results of Wilson and Boothroyd (1944) and those of the author after cold treatment are again the results of using different techniques as clearly indicated in table I, 2, 4, 6. In an attempt to explain this discrepancy the writer employed the aceto-carmines along with the Feulgen technique to obtain comparative data. The total length of the chromosome complement using the aceto-carmines technique on the root tips of the Tennessee plants of *T. erectum* L. is close to that listed for Wilson and Boothroyd (1944) (table I, 4, 6). The total length was 201.2 microns on *T. erectum* L. used in this study and  $234 \pm 4.5$  microns on the material of Wilson and Boothroyd (1944). In the writer's opinion this is not a very significant difference inasmuch as all measurements are slightly lower than those of Wilson and Boothroyd (1944).

Furthermore, it is again possible to compute ratios between the long and short arms of the chromosomes after cold treatment from the figures given by Wilson and Boothroyd (1944) and from the writer's data (table II). If these ratios are compared it will be found that very little variation exists between the two, that is, the ratios increased or decreased in about the same proportions in the two sets of figures (normal and cold treated).

It should be noted in passing that the ratios for chromosomes A, D, and E decrease slightly while for chromosomes B and C the ratios remain about the same after cold treatment.

The increase and decrease in the ratios seem to indicate that the differential segments undergo less contraction during cold treatment than do the non-affected portions of the chromosomes. Chromosome A which shows the greatest decrease in its ratio has in the long arm three regularly occurring differential segments, while none are present in the short arm. Chromosome C shows an increase in its ratio which may be accounted for by the fact that only one differential segment appears, namely that in the short arm. One differential segment appears in both the short and long arm of chromosome B, the one in the short arm being almost twice the length of the one in the long arm. This fact would account for the increase in the ratio just as in chromosome C. The differential segments are approximately the same length in the two arms of chromosome E, and, as expected, the ratio remains approximately the same.

Wilson and Boothroyd (1944) compared the length of chromosome arms which had differential segments with those having none to show that contraction produced by cold is not uniform throughout the chromosome complement. The results in the present study were similar. As was shown

in the preceding paragraph, the ratio of the length of the short arm to the long arm in chromosome C is 54:100 in untreated material and 61:100 in treated material. The corresponding ratios of B short to C long arm are 50:100 and 68:100 respectively.

It is significant that chromosome D shows the greatest degree of contraction of any of the chromosomes. The difference in the total length between the normal and treated chromosome is 5.4 microns. This can be accounted for, however, by the fact that 28.7% of the chromosomes do not show any differentially reactive segments. This means, as has been pointed out in the preceding paragraphs, that those chromosomes which did not show any differential segments underwent a greater degree of contraction. Actually their length after treatment was only 83.8% of the length before treatment.

A fact that has not been pointed out previously is that the primary constriction is actually a region which is differentially reactive. As shown in figures 1, 2, 3 and 4 the primary constrictions of untreated chromosomes appear to be very short. Figure 5 reveals them to be much longer after cold treatment. The length of the primary constriction is about the same as the regularly appearing differential segments in treated chromosomes. The diagrams of Wilson and Boothroyd (1944) do not show this to be true of their material. Actually this would mean that 10 more differential segments should be added to the number which appear regularly after treatment in the writer's material. This would make a total of 30 such segments.

The diagrams (fig. 5) depicting the range of differential patterns indicate that the length of the differential segments varies from 0.42 to 0.83 microns, the greater percentage of them being 0.83 microns.

Figure 5 indicates clearly the degree of variation in the differential segments. An accurate record was kept of every chromosome measured and the plant and root tip from which it came. Reference to these records reveals that not all chromosomes having a given differential pattern occur within the same plant or within the same root tip; any combination of differentially reactive segments shown in the diagrams illustrating the various patterns may occur.

Chromosome fragmentation was observed in this study in root tip mitoses of two different plants. The fragmentation, however, cannot be attributed to the cold treatment because the root tips of one plant were untreated, while those of the other had been exposed to cold. The chromosomes from root tips which had received no cold treatment were perfectly normal as to length, width, position of the primary constriction, etc. In no instance where chromosome fragments were present did chromosome D show any

intercalary segments. The two fragments when present were usually located on or very near chromosome D which may or may not have any significance.

No correlation was found between the number of visibly differentiated segments and the number of chromocenters in the resting nucleus with which Darlington and LaCour (1940) associated them. The maximum number of chromocenters counted was approximately 14 or 15 while the number of differential segments ranges from 20 to 24.

**Trillium luteum (Muhl.) Harbison.** The morphology of the normal chromosome complement of *T. luteum* (Muhl.) Harbison was studied using both the Feulgen and the aceto-carminic techniques. This study was made in order to determine whether the difference occasioned by the two different techniques in *T. erectum* L. would occur in another species of *Trillium*. The results of this phase of the study are also included in table I, 7 and 8. The total length of the chromosome complement is 193.6 microns in Feulgen preparations (fig. 3) while by the aceto-carminic technique the total length is 273.4 microns (fig. 4). If this result is expressed as a percentage, the total length with the Feulgen technique will be 71% of that obtained by the aceto-carminic technique. These results approach very closely those found with *T. erectum* L., the difference between the two techniques on *T. erectum* L. being 30%. This indicates that the difference between the two techniques may be constant. A pictorial comparison of the results of the two techniques may be observed in the photomicrographs (figs. 6-11); however, the chromosomes of figure 10 have undergone some stretching as a result of the squash technique. Certain chromosomes can be singled out which have apparently undergone no stretching and comparison may be made with these.

Another significant feature of this phase of the study is the similarity between the morphology of chromosomes of *T. erectum* L. and *T. luteum* (Muhl.) Harbison. The total length of the individual chromosomes of *T. erectum* L. by the Feulgen technique is 199.4 microns while the total length of those of *T. luteum* (Muhl.) Harbison using the same technique is 193.6 microns. These measurements are entirely too close to separate these species on the basis of total length of the chromosome set. There are differences between the long-short-arm ratios and in the total length of the individual chromosomes between the two species. Chromosomes A and B (figs. 1 and 3) show the greatest variations. The writer, however, is in agreement with Barksdale (1938) when he states that the view that minor floral and vegetative variations peculiar to any one species should be reflected in the morphology of one or several of the chromosomes is a rather naive one. Before the assumption can be made that different species of the genus *Trillium* can be separated on the basis of chromosome morphology, a very thorough cytological investigation must be made of every species within the genus.

## SUMMARY

1. Morphological differences exist in the normal chromosome complement of *T. erectum* L. growing in Tennessee and *T. erectum* L. growing in Canada. Taxonomically the plants are identical insofar as the conventionally employed morphological characters are concerned.

2. In obtaining valid comparative data as to chromosome morphology identical techniques must be employed. The Feulgen and the aceto-carmin techniques give results which differ by approximately 30% in the *Trillium* species studied. This is shown in both the study of *T. erectum* L. and *T. luteum* (Muhl.) Harbison. There is no difference with these techniques, however, as to the position of the primary constriction; the ratio between the long arm and short arm remains the same.

3. The pattern of differential segments produced by cold treatment cannot be employed as a valid or even useful taxonomic indicator for distinguishing species, for too many differences exist in the regularly recurring pattern in the Canadian *T. erectum* L. and that in plants of the same species growing in Tennessee.

4. The primary constriction also behaves like a region of differential reactivity upon exposure to cold.

5. The differential segments themselves undergo less contraction than the non-affected portions of the chromosomes upon exposure to cold.

6. The morphology of the normal chromosomes set of *T. erectum* L. differs slightly from that of *T. luteum* (Muhl.) Harbison; however, the total length of the two complements is the same.

## ACKNOWLEDGMENT

The writer wishes to take this opportunity to express his appreciation to the late Dr. Thomas M. Woodard, Jr., who suggested this study and under whose direction most of it was carried on. He also wishes to express his gratitude to Dr. Harold C. Bold for suggestions and criticisms in the completion of the problem and in preparation of the manuscript. Thanks are also due to Dr. Frederick T. Wolf for reading and criticizing the manuscript.

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## RANGE EXTENSIONS OF *CAREX NEUROCHLAENA* HOLM

MAXIMILIAN G. DUMAN

*Carex neurochlaena* was described by Holm (1904) from specimens collected by Macoun above Rink Rapids on the Yukon River, Yukon. After its description it was unreported for nearly forty years until collections from both eastern and western Canada were reported nearly simultaneously. Eighteen collection numbers made by Dutilly, O'Neill, and the author in eastern Canada at Wakeham Bay, Churchill, Chesterfield, Baker Lake, and Repulse Bay were reported by Duman (1941). Hultén (1942) refers to the collections of A. E. Porsild, and gives its range "from Yukon to the N. W. Territories." He does not include it in the flora of Alaska. Porsild (1943) cites seven collection numbers, and gives its range in the Northwest Territories "from the Mackenzie River Delta east to Anderson River, south to Great Bear Lake."

A short discussion of the status and distribution of *Carex neurochlaena* appeared in this BULLETIN two years ago (Duman 1947). Since that time the identification of several noteworthy collections made by Arthème Dutilly, Hugh O'Neill, and Ernest Lepage has extended its range south into the James Bay region, north into Baffin Island, and west into Alaska.

In 1942 Dutilly collected a single specimen of *Carex neurochlaena* at Lake Harbor, Baffin Island (*Dutilly 9125a*). This is a new addition to the flora of Baffin Island.

During the summer of 1946 Dutilly and Lepage collected *Carex neurochlaena* on the west coast of James Bay at Lake River (*Dutilly & Lepage 16579, 16672*), and at Fort Albany (*Dutilly & Lepage 16011*). This is a southern extension of range for this northern species.

In 1947 Dutilly, O'Neill and Lepage collected *Carex neurochlaena* at Nebesna Road, Mile Post 91, Alaska (*Dutilly, O'Neill & Lepage 21605*). This location is just across the Alaska-Canadian border from the type locality in the Yukon. In 1948 Lepage collected this species at Umiat, Colville River (69° N. Lat.), Alaska (*Lepage 23775*). These are the first reported collections from Alaska, and hence represent a new addition to the flora of Alaska.

Lepage (personal communication) confirms our observation that solitary culms growing in wet sphagnum are characteristic of this inland species, and suggests that this may be one of the reasons that it has been frequently overlooked.

In some of the collections made before this species was recognized in the field the material is rather scarce, as would be expected in a species



with scattered culms. In other localities, however, it is far from being rare, as for example the abundant material in the ten collection numbers made by Dutilly and the author at Churchill. Lepage informs us that it is commonly scattered through the sphagnum bogs at Umiat, Alaska.

Although this species is now known over a wide range, the collection localities are widely separated. Undoubtedly a careful search in wet sphagnum bogs for its solitary, scabrous culms, bearing green to brown perigynia which are gradually smooth-beaked, the beak having a very characteristic slight bend, will uncover new stations, and give us a more true picture of the actual distribution of this interesting species.

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## CRITICAL NOTES ON SOME PLANT RUSTS

M. J. THIRUMALACHAR

1. On *Scopellopsis Dalbergiae* Ramk. & Ramk. and *Mainsia Pterocarpi* Thirum. The genus *Scopellopsis* was established by Ramakrishnan and Ramakrishnan (1947a) for a rust on *Dalbergia paniculata* Roxb. Subepidermal uredia and intraepidermal telia with one-celled, stipitate, colourless spores borne on basal cells were given as important characters. Thirumalachar (1947) described the rust *Mainsia Pterocarpi* earlier from Mysore, South India. A careful restudy of *Scopellopsis Dalbergiae* and *Mainsia Pterocarpi* indicated that the two rusts were identical, and the hosts probably closely related. In a recent paper Thirumalachar and Cummins (1949) discussed the taxonomic significance of sporogenous basal cells in the Uredinales and concluded that the clustered condition only represented one of the modes of spore development, without having generic significance. Evidence was presented for not maintaining the genus *Scopellopsis*.

Thirumalachar (1947) described the same rust as *Mainsia Pterocarpi* because of the intraepidermal telia and the hyaline, stipitate teliospores. The genus *Mainsia* Jackson, however, includes both forms with intraepidermal and with superstomal sori, the latter resembling *Gerwasia* Racb. Further studies are needed to elucidate and stabilize its generic characters. Though pycnial stages are known for *Scopellopsis Dalbergiae*, its resemblance to *Maravalia achroa* (Syd.) Arth. & Cumm. is close. In the collections of *Maravalia achroa* made by Clemens in the Philippines there are distinct sporogenous basal cells in the telia. The only differentiating features in *Maravalia achroa* are the lack of paraphyses and the subepidermal position of the telia. Pycnial stages will be necessary to confirm whether the rust is a species of *Maravalia* or of *Scopella*. For the present, to indicate the close relationship between the two rusts, the species on *Dalbergia paniculata* is placed under *Maravalia*: ***Maravalia Pterocarpi* (Thirum.) Thirum. comb. nov. (*Mainsia Pterocarpi* Thirum., *Scopellopsis Dalbergiae* Ramk. & Ramk.)**

2. On *Maravalia ascotela* (Syd.) Mains. In a recent study, Ramakrishnan & Ramakrishnan (1947b) have discussed the need for a change of nomenclature of *Maravalia ascotela* (Syd.) Mains (Mains 1939) which had been transferred to *Chrysocelis ascotela* by Thirumalachar (1942a), on the basis of a cytological study. Ramakrishnan & Ramakrishnan noted the basal cells and transferred the rust to *Scopella* as *S. ascotela* (Syd.) Ramk. & Ramk. Since the rust has subepidermal pycnia, in contrast to the subcuticular ones found in the type of the genus, they emended the generic de-

scription of *Scopella* Mains to include both subepidermal and subcuticular pycnia, citing as supporting evidence the example of *Ravenelia* which has been referred to (Thirumalachar & Cummins 1949). The emendation of the genus is undesirable since it is the pycnial character that is of primary importance and the presence of basal cells is secondary only. Since the elongation of the basal cells into pedicel-like structures can be traced only in well-stained microtome preparations, it seems advisable for taxonomic purposes to follow Mains' (1939) treatment.

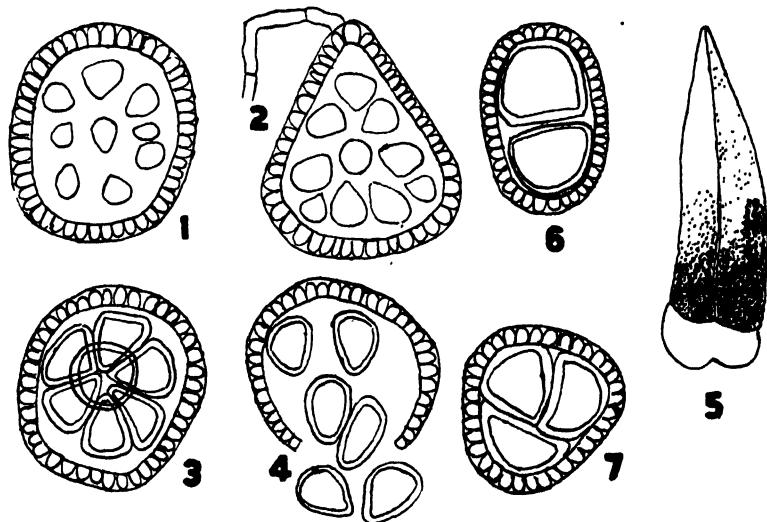
**3. On *Mehtamyces* Mundkur & Thirum.** The genus *Mehtamyces* was established for a rust on *Stereospermum suaveolens* Wall. in India by Mundkur & Thirumalachar (1945). The genus is characterized by the presence of aparaphysate uredia with urediospores borne in clusters on sporogenous basal cells, and non-erumpent, subepidermal telia developing as large indefinite crusts. The teliospores are produced in chains of 4-8 spores, yellowish-brown in color and compactly grouped. Since the sporogenous basal cells, either within the uredia or telia, have been shown to be without generic significance, the rust was restudied.

The telia provide the chief differentiating character. The telial crusts externally resemble the type found in many species of *Pucciniastrum*, such as *P. Coriariae* Diet. and *P. Castaneae* Diet. in forming large indefinite patches. Some of the telia on *Stereospermum* leaves measure up to 3 cm. Telia of this type are quite distinct from the lenticular crusts found in the genera *Phakopsora* Diet., *Angiopsora* Mains, and *Bubakia* Arth. Even the initial stages of telial development somewhat resemble that of *Pucciniastrum* species, as described by Pady (1933). The telial initials are formed between the epidermis and palisade layers. In *Pucciniastrum*, a series of vertical septations takes place resulting in a flattened telial crust, while, in *Mehtamyces*, these produce vertical chains of spores in basipetal succession. Further, in *Mehtamyces*, the teliospores are resting spores, and the uredia are without the characteristic peridium of *Pucciniastrum*. Therefore, even if the sporogenous basal cells of the uredia are disregarded, the telial characters separate the genus *Mehtamyces* from other genera.

**4. *Puccinia* on *Chomelia asiatica* O.Kze.** A rust on *Chomelia asiatica* was described by Thirumalachar (1942b) as a new species under the name *Puccinia Chomeliae*. A comparative study of *Puccinia spongiosa* Berk. & Br., deposited in the Arthur Herbarium and in the Mycological Collections of the U.S.D.A., indicates that the two resemble each other closely. Slight variations in the sizes of the teliospores have been noticed in some of the collections but considering the general range of variability, it is desirable to merge *P. Chomeliae* Thirum. with *P. spongiosa*.

**5. On *Uleiella* Schroet.** The genus *Uleiella* was founded by Schroeter (1894) for a fungus parasitic on shoots of *Araucaria imbricata* in Brazil,

collected by Ule. The fungus forms sooty black spore mass within the host tissue. The spores are subglobose to spherical, chestnut-brown, and inclosing 6-8 sporidia (?). *Uleiella paradoxa* Schroet. was designated as the type, and the fungus was placed under the Uredinales. Saccardo (1897) in listing the genus, doubtfully assigned it under the smuts. Another species, *Uleiella chilensis* Diet. & Neger (1899), was established for a similar fungus on *Araucaria imbricata* in Chile. Dietel (1897-1900), in his treatment of the "Hemibasidii", briefly described the development of the spores within the host at the ends of hyphae. Though the spores have not been germinated, Dietel considered the genus as a doubtful member of the Hemibasidii along with *Meria* Vuillemin, which was once placed under that order. However, recent studies have shown that *Meria* is a moniliaceous fungus.



FIGS. 1-4. Developmental stages of the spores of *Uleiella paradoxa*.  $\times 300$ . FIG. 5. Sporophyll of *Araucaria imbricata* showing infection.  $\times 1$ . FIGS. 6, 7. Spores of *Uleiella chilensis*.  $\times 300$ .

Authentic specimens of *Uleiella paradoxa* and *U. chilensis* (Rabenhorst-Winter-Pazschke, *Fungi Europaei* 3940 and Rabenhorst-Pazschke, *Fungi Europaei et Extraeuropaei* 4303) deposited in the Mycological Collections of the U.S.D.A. were studied. Sections through the infected sporophylls (fig. 5) of *U. paradoxa* revealed that the spores develop from the hyphae bordering the lacunae formed within the host tissue. The spores are spherical to subglobose, yellowish to chestnut-brown, and with a deeply pitted spore wall which imports a tuberculate appearance. As the spores mature, 6-14 small endospores appear within the spore cavity. These are at first scattered (figs. 1, 2) but as they enlarge in size, they occupy the entire space (figs.

3, 6, 7). The endospores are somewhat angular due to mutual compression. In later stages, the outer sporecoat bursts and releases the endospores (fig. 4). The mode of development of the endospores resembles the free cell formation within an ascus, though it is not possible to get all the details from herbarium material.

The genus *Uleiella* has been doubtfully placed under either rusts or smuts by Schroeter, Dietel, Saccardo, Ainsworth & Bisby (1945), and others. The morphology of the spores indicates that it does not belong to either of them.

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## HYBRID OF *KALANCHOË DAIGREMONTIANA* AND *K. VERTICILLATA*

J. T. BALDWIN, JR.

A photograph of two *Kalanchoë* species and their hybrid appeared in the *Cactus and Succulent Journal* for August, 1939 (11: 64). Though the plants were young, the parents were obviously referable to *K. Daigremontiana* Hamet & Perrier and *K. verticillata* Scott-Elliot, and the hybrid seemed intermediate in leaf characters. It was known that *K. Daigremontiana* is a diploid biennial or triennial and that *K. verticillata* is a tetraploid perennial (Baldwin 1938). The report of a hybrid between them was therefore of peculiar interest.

Scott E. Haselton, Editor of the *Cactus and Succulent Journal*, wrote (letter of April 24, 1940) that the hybrid had been made by Dr. A. D. Houghton (then deceased), whose gardens were in San Fernando, California, and from those gardens Mr. Haselton sent me parental and hybrid plants. The hybrid was more intermediate than the photograph had revealed.

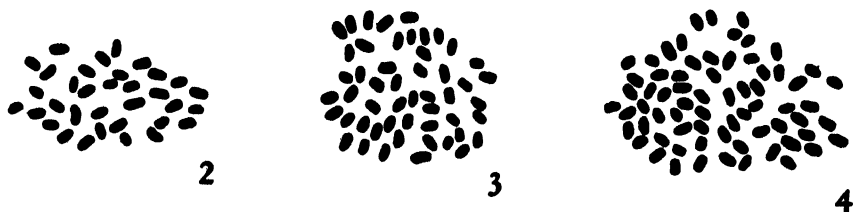
Detailed comparison of the two species and their hybrid was planned. And for that reason plants were obtained from several sources. But the project was interrupted during the war years, and on resumption of work it was discovered that the gardener had discarded from the greenhouse all of these highly efficient weeds. And who could blame him? Swingle (1934) called *H. Daigremontiana* "the easiest plant in the world to propagate." The hybrid and its other parent, however, are just as readily multiplied. Plantlets are produced in great quantities on the leaves of all the individuals concerned.

Because the hybrid is undoubtedly well established in American horticulture (it was, for example, found in a Roanoke, Virginia, greenhouse), and because the hybrid and its parents are excellent experimental material, a drawing of the hybrid made by Eduardo Salgado is published here (fig. 1).

Baldwin (1938) reported *K. Daigremontiana* to have  $2n = 34$ ,  $n = 17$  and *K. verticillata* to have  $2n = 68$ . Uhl (1948) recorded  $n = 17$  in *K. Daigremontiana*. This species as sent me by Mr. Haselton had  $2n = 34$  (fig. 2); *K. verticillata*,  $2n = 68$  (fig. 4); the hybrid,  $2n = 51$  (fig. 3). As expected, the hybrid was triploid and thus intermediate between its parents. The hybrid from Roanoke, Virginia, was likewise triploid. *K. Daigremontiana* from other sources in California and Texas was diploid, and *K. verticillata* from other sources in California and from Michigan State College was tetraploid. The chromosome numbers determined for these two species are apparently constant. But all the representatives of each species in the United States are



FIG. 1. *Kalanchoe Daigremontiana*  $\times$  *K. verticillata*, drawn natural size by Eduardo Salgado and reduced to  $\times 0.5$  in reproduction.



FIGS. 2-4. Chromosomes of parents and hybrid in *Kalanchoë*. FIG. 2.  $2n=34$  in *K. Daigremontiana*. FIG. 3.  $2n=51$  in the hybrid. FIG. 4.  $2n=68$  in *K. verticillata*.  $\times 4900$ .

likely to be the products in each case of single-plant introductions into the country. If in nature *Kalanchoë* follows the pattern determined for most of the Crassulaceae that have been subjected to extensive cytogeographic analysis, it would not be surprising to find more than one intraspecific chromosomal race in any given species.

*Kalanchoë*, with perhaps more than a hundred valid species, is fairly popular in the United States. "The species exhibit a wide range of characters, though the plants are much alike in their chromosomal make-up. *Kalanchoë* appears, therefore, to be an excellent group to hybridize inter-specifically. The flowers would offer no technical difficulty in breeding experiments. Valuable hybrids could be preserved by vegetative means. The genus, no doubt, has a future of real horticultural interest" (Baldwin 1938).

#### SUMMARY

Dr. A. D. Houghton made a hybrid some years ago in California of *Kalanchoë Daigremontiana* ( $n = 17$ ,  $2n = 34$ ) and of *K. verticillata* ( $2n = 68$ ) that is triploid ( $2n = 51$ ) and has intermediate characters. That hybrid is in the American horticultural trade.

*Kalanchoë* is a promising genus for interspecific hybridizing.

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## CYTOGEOGRAPHY OF EMILIA IN WEST AFRICA

J. T. BALDWIN, JR. AND BERNICE M. SPEESE

Garabedian (1924), in the most recent revision of *Emilia* Cass., recognized twenty-three species and regarded *Emilia* "more as an association of allied species than as a distinct genus." It has close affinities with *Gynura* and *Senecio* and is difficult to interpret from herbarium material alone. As seed become available we plan to grow the various representatives of this genus and to investigate their chromosomes.

Afzelius (1924) reported  $n$ -numbers of 5 chromosomes for *E. sagittata* (Vahl) D. C. and for *E. sonchifolia* (L.) DC. Baldwin (1946) recorded that  $2n = 10$ ,  $n = 5$ , for *E. sonchifolia*, and  $2n = 20$  for *E. coccinea* (Sims) Sweet and discussed the cytogeographic occurrence of these two species in the Americas.

During 1947-1948, as Horticulturist, Economic Mission to Liberia, U. S. Department of State, the senior author travelled extensively in West Africa and, incidental to his assignment there, observed *Emilia* and made a few collections. Plants for cytological study have been grown in our greenhouse at the College of William and Mary. Specimens will be deposited in the herbaria of several institutions: Royal Botanic Gardens at Kew, Jardin Botanique de l'État at Brussels, U. S. National Arboretum, Smithsonian Institution.

Hutchinson and Dalziel (1931) listed three species of *Emilia* for tropical West Africa: *E. sagittata*, *E. sonchifolia*, and *E. guineensis* Hutch. & J. M. Dalziel. Baldwin examined at Kew the type of the last-named species (*Caille 14702*, Bowal to Bouria, French Guinea, Nov. 1905) and judged the specimen not referable to *Emilia*. In the opinion of Dr. R. Fosberg the plumose pappus and imbricate involucre of *Caille 14702* prevent inclusion of the specimen under *Emilia* (conversation). Hutchinson and Dalziel (1931) cited six collections for *E. guineensis*, all from French Guinea, and made *Lactuca tenerrima* A. Chev. synonymous with it; no further mention will be made by us of this entity. *Emilia* sp. is included here as an addition to the West African flora.

Of the three representatives of *Emilia* accepted for West Africa only *E. sagittata* seems not to be a weed. This species is widely distributed as an integral part of the flora. Along the trails in Liberia or beside the roads in French Guinea and along those leading inland from the coast of Nigeria, the cadmium yellow heads of *E. sagittata* frequently attract attention. But during the dry season—December to March in Liberia—this species is rarely in flower. Usually small populations of this plant occur, but some-

times a single individual is present. And in August 1947, a few miles east of Tappita, in the Eastern Province of Liberia, Baldwin saw thousands of flowering plants of this species growing among marsh vegetation. The plant itself, aside from its striking flowers, is not attractive: it stands laxly erect and when among other herbs may rise to several feet. The following collections were made:

*Baldwin 5933* Liberia: Montserrado Co.: between Monrovia and Harbel, June 6, 1947. *7099* Liberia: Eastern Province: Tchien District: Monrovia-town, August 10, 1947. *9747* French Guinea: midway between N'Zérékoré and Macenta, October 13, 1947. *12012* Nigeria: Abeokuta, April 28, 1948.

Seedlings from *Baldwin 5933* were grown, and their chromosomes investigated by Speese:  $2n = 10$ ,  $n = 5$  (figs. 1-3). These results agree with previous reports.

*E. sonchifolia* is a widespread weed in tropical areas and is generally considered to be of Old World origin. However, in most of West Africa it is not common. Although Baldwin walked throughout Liberia (with an area of about 37,000 square miles), he found only three small populations of this species. There the plant seems restricted to sandy soils largely free of other plants and in the vicinity of coastal towns. In the Americas *E. sonchifolia* is often in comparable situations, but it is sometimes far inland, as in the Amazon Valley (Baldwin 1946). And at some places it competes rather well with other species: it was, for example, observed in 1947 among rank vegetation beside the airfield at São Luis de Maranhão in Brazil.

At first thought the extremely limited distribution of *E. sonchifolia* in Liberia is surprising, for over the centuries the natives have engaged in a "shifting agriculture" whereby ecological situations seemingly favorable for this weed have been created in abundance. But unless the human population is dense enough to carry on intensive cultivation, "bush rotation" would not be conducive to establishment of this weed. Fortunately for conservation reasons this has not been true: the native population is estimated to be under a million individuals. Moreover, it has been discovered (Baldwin 1946) that *E. sonchifolia* tends to spread along routes of considerable travel. The Liberian native has been hesitant to go beyond tribal boundaries. And the Americo-Liberians—settled along the coast and probably numbering about ten thousand—have mostly travelled to Europe and North America, where *Emilia* does not occur. Until the harbor at Monrovia was opened in 1948, coastwise steamers could not come in to shore along the Liberian coast. In contrast to Liberia, a dense human population in the Gold Coast and Nigeria, with consequent greater travel and more intensive agriculture, would explain the more frequent occurrence of this weed in those countries.

The flowers of *E. sonchifolia* fall within the purple-red color group. The color, approximating mallow pink, seems constant. Plants vary consider-

ably in size depending on conditions for growth. Our concept of the species, illustrated by Baldwin (1946), encompasses the type of *Cacalia sonchifolia* as well as that of *Cacalia lyrata*; those types were examined in the Linnaean Herbarium in London.

The following collections of *E. sonchifolia* were made:

*Baldwin 5998* Liberia: Maryland Co.: Harper, June 14, 1947. *11219* Liberia: Grand Bassa Co.: Timbo, March 6, 1948. *11570* Liberia: Sinoe Co., Greenville, March 18, 1948. *11986* Ivory Coast: Abidjan, April 12, 1948. *11990* Gold Coast: Aburi: old botanical garden, April 17, 1948. *12525* Gold Coast: Accra: Achimota College, April 16, 1948. *11980* Nigeria: Agege (near Lagos): agricultural experiment station, April 28, 1948. *12524* Nigeria: Benin City: Oil Palm Research Station, May 3, 1948.

Baldwin likewise saw this species at Freetown, Sierra Leone, May 29, 1947.

Seedlings represented by *Baldwin 11990*, *12524*, and *12525* were grown, and their chromosomes studied by the junior author:  $2n = 10$  (Accra material),  $n = 5$  (Aburi material) (figs. 4-6). These results corroborate previous work.

At the Agege agricultural experiment station near Lagos, Nigeria, the senior author on April 28, 1948, collected specimens of *Emilia* which did not fit into the generic treatment of Hutchinson and Dalziel (1931) for West Africa: *Baldwin 11981*. The plants grew to a height of eighteen inches and had yellowish white corollas tipped with orange-red. Existence of these weeds at an agricultural station, which had been established in 1910, suggested the likelihood of accidental introduction there with seed of some economic plant.

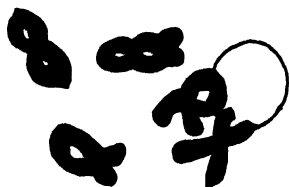
Dr. S. F. Blake, relying on Garabedian's generic treatment, identified one of the Agege specimens as *E. sagittata* (letter of October 5, 1948). Dr. W. Robyns reported (letter of November 6, 1948) that the plant seemed to be *E. sonchifolia* var. *mucronata* Clarke and added (letter of December 15, 1948) that, though near *E. sonchifolia*, the Agege material matched no Brussels specimen exactly. Mr. E. Milne-Redhead (letter of December 20, 1948, from the Director, Kew) was unable to determine the Agege plant but found it to agree with two collections from Freetown, Sierra Leone, which, in his opinion, had been erroneously referred to *E. sagittata*, "a species from which they differ in having strongly toothed leaves, longer involucre bracts and pale yellow flowers."

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FIGS. 1-10. Chromosomes of *Emilia*. FIGS. 1-3. *E. sagittata*:  $2n = 10$  in leaf smear and  $n = 5$  at diakinesis I and metaphase I of microsporogenesis. FIGS. 4-6. *E. sonchifolia*:  $2n = 10$  in leaf smear and  $n = 5$  at diakinesis I and metaphase I. FIGS. 7-8. *Emilia* sp.:  $2n = 20$  in leaf smear and  $n = 10$  at metaphase I. FIGS. 9-10. *E. coccinea*:  $2n = 20$  in leaf smear and  $n = 10$  at metaphase I. All figures  $\times 2200$ .



1



2



3



4



5



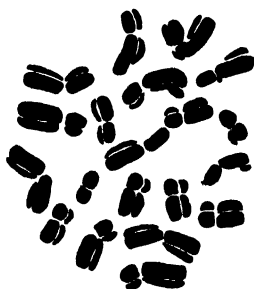
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7



8



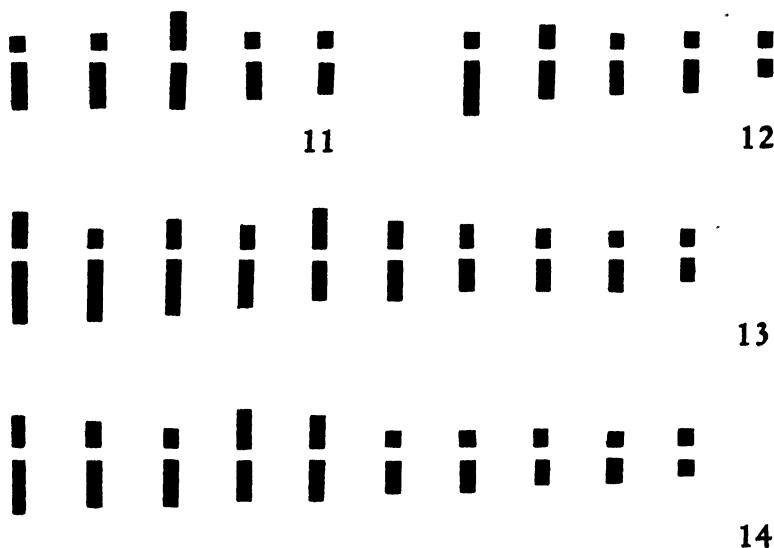
9



10

Seedlings of *Baldwin 11981* have been grown. Speese finds them to have a  $2n$ -number of 20,  $n$ -number of 10 (figs. 7-8). They are, therefore, tetraploid. E. Milne-Redhead (letter of June 20, 1949) sent seed of two collections from Sierra Leone that seemed to match *Baldwin 11481*: *F. C. Deighton s.n.* and *H. C. King 182*; seedlings from both collections are tetraploid.

*E. coccinea* from Rio de Janeiro (*Baldwin 4578*) is likewise tetraploid (figs. 9-10). Interesting in this regard is that this species is an effective greenhouse weed, whereas diploid *E. sonchifolia* is not. No information is available relative to this for other members of the genus.



FIGS. 11-14. Idiograms of *Emilia* chromosomes. FIG. 11. *E. sagittata*. FIG. 12. *E. sonchifolia*. FIG. 13. *Emilia* sp. FIG. 14. *E. coccinea*.

To determine whether or not chromosome morphology might afford data on phyletic affinities of the four *Emilia* representatives now cytologically known, idiograms of the chromosomes were made (figs. 11-14). Those idiograms demonstrate that neither the Agege plant nor *E. coccinea* is an autotetraploid of *E. sonchifolia* or of *E. sagittata*. No statement about affinities between the two tetraploids can as yet be given except to say that they do appear to have certain chromosomes in common and that under greenhouse conditions they somewhat resemble each other.

#### SUMMARY

Three representatives of *Emilia* occur in West Africa, and one plant (*E. guineensis*) is considered to have been erroneously referred to this genus. One representative of the genus is reported here for the first time as

an element of the West African flora; its proper designation has not been determined.

Mitotic and meiotic analyses were made for the three West African plants: two were diploid ( $2n = 10$ ,  $n = 5$ ), one tetraploid. Idiograms of chromosomes give no evidence of phyletic relations. But the tetraploid seems to have some affinity to *E. coccinea* which, as a tetraploid, is a tropical American weed and which is the only other cytologically known representative of the genus.

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THREE NEW SPECIES OF CHYTRIOMYCES  
FROM MARYLAND<sup>1</sup>

JOHN S. KARLING

The present contribution concerns three additional species of *Chytriumyces* which were discovered in the course of a survey of the soil fungi of Maryland. Members of this genus are characterized by monocentric encarpic thalli with extramatrical resting spores and operculate sporangia, intramatrical rhizoids which may or may not arise from a subsporangial apophysis, and zoospores which in most species swarm in a vesicle outside of the sporangium. The new species from Maryland have these general characteristics but differ specifically from the known members of the genus primarily by zoospore size, character of the rhizoids, presence or absence of an apophysis, and the structure of the resting spore.

The first of these species to be described parasitizes *Closterium rostratum* and is distinguishable primarily by its small zoospores. It is, accordingly, named *Chytriumyces Closterii*. The other two species are saprophytic and were isolated from soil and water and grown on cellulosic and chitinic substrata. One of these species is characterized by coarse, rigid, and stiff-looking rhizoids, smooth resting spores, and by unusually large hyaline refractive globules in the mature sporangia and zoospores which give them a strikingly refringent or glistening appearance. Because of the latter characteristic it is named *C. lucidus*. The other species has spiny to verrucose and echinulate resting spores, apophysate sporangia, and very bushy rhizoids. The latter give the thalli a distinctive bushy appearance, and for this reason it is named *C. fruticosus*.

***Chytriumyces Closterii* Karling, sp. nov.** Fungus parasiticus. Sporangii hyalinis, laevibus, non apophysatis, sphaericis, 5-25  $\mu$  diam., pyriformibus, 6-19  $\times$  9-24  $\mu$  diam.; operculo apicali, 4-6  $\mu$  diam. Zoosporis sphaericis, 2-2.5  $\mu$ , diam., globulo refractivo hyalino, 0.4-0.6  $\mu$  diam.; flagello 9-12  $\mu$  longo. Sporis perdurantibus hyalinis, laevibus, sphaericis, 7-12  $\mu$  diam., aut ovalibus germinantibus zoosporangia tenui membranata superficialia generentibus.

Sporangia hyaline, smooth, non-apophylate, spherical, 5-25  $\mu$ , or broadly pyriform, 6-19  $\times$  9-24  $\mu$ , with one apical exit papilla; operculum shallow saucer-shaped, 4-6  $\mu$  diam., non-persistent. Zoospores spherical,

<sup>1</sup> This study was begun at the Chesapeake Biological Laboratory, Solomons, Md., where the writer was guest investigator during the spring and early summer of 1948. The author is very grateful to the Department of Research and Education, State of Maryland, and particularly to the Director of the Laboratory, Dr. R. V. Truitt, for providing research facilities and funds for this work.

2–2.5  $\mu$ , with a minute, 0.4–0.6  $\mu$ , hyaline refractive globule; flagellum 9–12  $\mu$  long; swarming actively in a vesicle outside of the sporangium. Single rhizoidal axis attached at base of sporangium, sparsely branched and sometimes extending for a distance of 120  $\mu$ . Resting spores hyaline, smooth, 7–12  $\mu$ , or oval with a large central globule surrounded by several smaller ones; content emerging through a pore in the wall during germination and forming a superficial sporangium.

Weakly parasitic on *Closterium rostratum* from a ditch along road to Drum Point Beach, Calvert County, Md.

**Chytriumyces lucidus** Karling, sp. nov. Fungus saprophyticus. Sporangia hyalinis, laevibus, non-apophysatis, subsphaericis, aut elongatis, 18–44  $\times$  28–66  $\mu$  diam., aut reniformibus; operculo apicali, 4–8  $\mu$  diam., hypocrateriformi demum evanescenti. Zoosporis ovalibus, 5.8  $\times$  6.2  $\mu$  diam., globulo refractivo hyalino, 3.6–3.9  $\mu$  diam. Hyphis rhizomorphis ramosis, crassiusculis, 4–12  $\mu$  diam. Sporis perdurantibus hyalinis, laevibus, ovalibus aut elongatis, 15–18  $\times$  20–25  $\mu$ ; germinatione ignota.

Sporangia hyaline, smooth, non-apophysate, usually flattened and elongated transversely to rhizoidal axis, 18–44  $\times$  28–66  $\mu$ , often almost hemispherical, or reniform, with one low, 3–4  $\mu$  high by 6–15  $\mu$  broad, apical exit papilla; operculum very shallow saucer-shaped, 4–8  $\mu$  diam., usually non-persistent. Zoospores slightly oval, 5.8  $\times$  6.2  $\mu$ , with a large hyaline, spherical, 3.6–3.9  $\mu$ , refractive globule. Rhizoids coarse, rigid and stiff-looking, main axes 4–12  $\mu$  in diam., often extending for a distance of 400  $\mu$  and becoming thick-walled with age. Resting spores hyaline, smooth, oval, slightly elongate, 15–18  $\times$  20–25  $\mu$ , with numerous angular refractive bodies; germination unknown.

Saprophytic in cellulosic substrata in soil and water along road to Drum Point Beach, Md.

**Chytriumyces fruticosus** Karling, sp. nov. Fungus saprophyticus. Sporangia hyalinis aut subfuscis, laevibus, plerumque apophysatis et appendiculatis, subsphaericis, 17–35  $\mu$  diam., aut ovalibus, 31–42  $\times$  37–50  $\mu$  diam., aut hemisphaericis, 15–55  $\mu$  diam., aut pyriformibus, aut obclavatis, aut citriformibus, aut elongatis; 1–2 papillis aut tubulo, 8–12  $\times$  10–60  $\mu$ , exeuntibus; operculo 4–8  $\mu$  diam., evanescenti. Zoosporis ovalibus, 3.8–4.2  $\times$  5.5–6  $\mu$  diam., globulo refractivo hyalino, 1.2–1.8  $\mu$  diam. Apophysis sphaericis, 8–20  $\mu$  diam., fusiformibus 14–16  $\times$  20–30  $\mu$ , irregularis, aut angularibus. Hyphis rhizomorphis fruticosus, crassiusculus, 3–8  $\mu$  diam., aut tenuissimis. Sporis perdurantibus subfuscis, spinosis aut verrucosis, sphaericis, 18–30  $\mu$  diam., aut ovalibus, aut angularibus; germinatione ignota.

Sporangia hyaline to light brown, often appendiculate and usually apophysate, variable in size and shape, almost spherical, 17–35  $\mu$ , oval, 31–42  $\times$  37–50  $\mu$ , almost hemispherical, 15–55  $\mu$  diam., broadly and narrowly pyriform, obclavate, citriform, elongate, or slightly anatrope, with 1–2 low exit papillae or 1–3 tapering exit tubes, 8–12  $\mu$  broad at the base by 10–60  $\mu$  long. Operculum saucer- to bowl-shaped, 4–8  $\mu$  diam., non-persistent. Zoospores oval, 3.8–4.2  $\times$  5.5–6  $\mu$ , with a hyaline, spherical, 1.2–1.8  $\mu$ , refractive globule; swarming actively and briefly in a vesicle outside of the sporangium. Apophysis variable in size and shape, rarely spherical, 8–20  $\mu$ ,



oval,  $8-15 \times 20-25 \mu$ , fusiform,  $12-15 \times 27-30 \mu$ , elongate,  $18-20 \times 30-32 \mu$ , irregular or angular. Rhizoids bushy in appearance and frequently branched, angles of branching obtuse and frequently at right angles; main axes centered on the base of the apophysis or arising at several points on the periphery,  $3-8 \mu$  in diam., branches occasionally extending for a distance of  $275 \mu$ . Resting spores light amber to greenish brown, usually spiny, occasionally verrucose or echinulate; spines up to  $15 \mu$  long by  $3 \mu$  wide at base; spherical,  $18-30 \mu$ , including spines, oval or slightly angular, with finely granular content; germination unknown.

Saprophytic on chitinous substrata in soil and water along route 505, Calvert County, Md.

**CHYTRIOMYCES CLOSTERII.** This species occurred in a collection of *Draparnaldia glomerata* and other algae which were brought into the laboratory on March 31, 1948. It does not appear to be a virulent parasite because it usually attacked *Closterium rostratum* only after this desmid had been kept in the laboratory for several days and become moribund. However, in a few cases healthy desmids were attacked and killed. So far it appears to be limited in host range to *C. rostratum*. It was never found to attack other species of *Closterium*, *Spirogyra*, *Mougeotia*, *Oedogonium*, *Vaucheria*, *Stigeoclonium*, or *Draparnaldia glomerata* which were growing in the same dishes with the parasitized *C. rostratum*.

In exceptional cases as many as 20 parasites may be found on a single host cell, but in most instances only 1-9 parasites are present (fig. 1). The parasite does not cause any enlargement or malformation of the host cell as in the case of *Chytriumyces parasiticus* (Karling 1947a). However, as the rhizoids elongate and branch the chloroplast, starch grains, and other parts of the protoplasm became clumped around them (fig. 1). Eventually, a large portion of the protoplasm is absorbed, while the remainder degenerates.

Of the known species of *Chytriumyces*, *C. Closterii* resembles *C. parasiticus* most closely by its small thalli, but it differs specifically from this species by its smaller zoospores (fig. 2), lack of an apophysis, and more extensive rhizoids. The latter may often be filled with refractive globules. In other respects, structure, and method of development, *C. Closterii* is fundamentally similar to other species of *Chytriumyces* and need not be described further.

**CHYTRIOMYCES LUCIDUS.** This species developed on small bits of onion skin, grass leaves, and to a limited extent on cellophane, but so far it has not grown on chitin. It is distinguished primarily by its large zoospores (fig. 13) which contain an unusually large refractive globule, very stiff and rigid-looking rhizoids (fig. 6), and by hyaline, smooth resting spores (figs. 15-17). Its zoospores are approximately the same size and shape as those

of *C. appendiculatus*, but the included refringent globule is usually twice as large. The size of the globules is such that in mature sporangia they appear to be packed together with very little space between them (figs. 6-10), which gives the sporangia a brilliant refractive appearance.

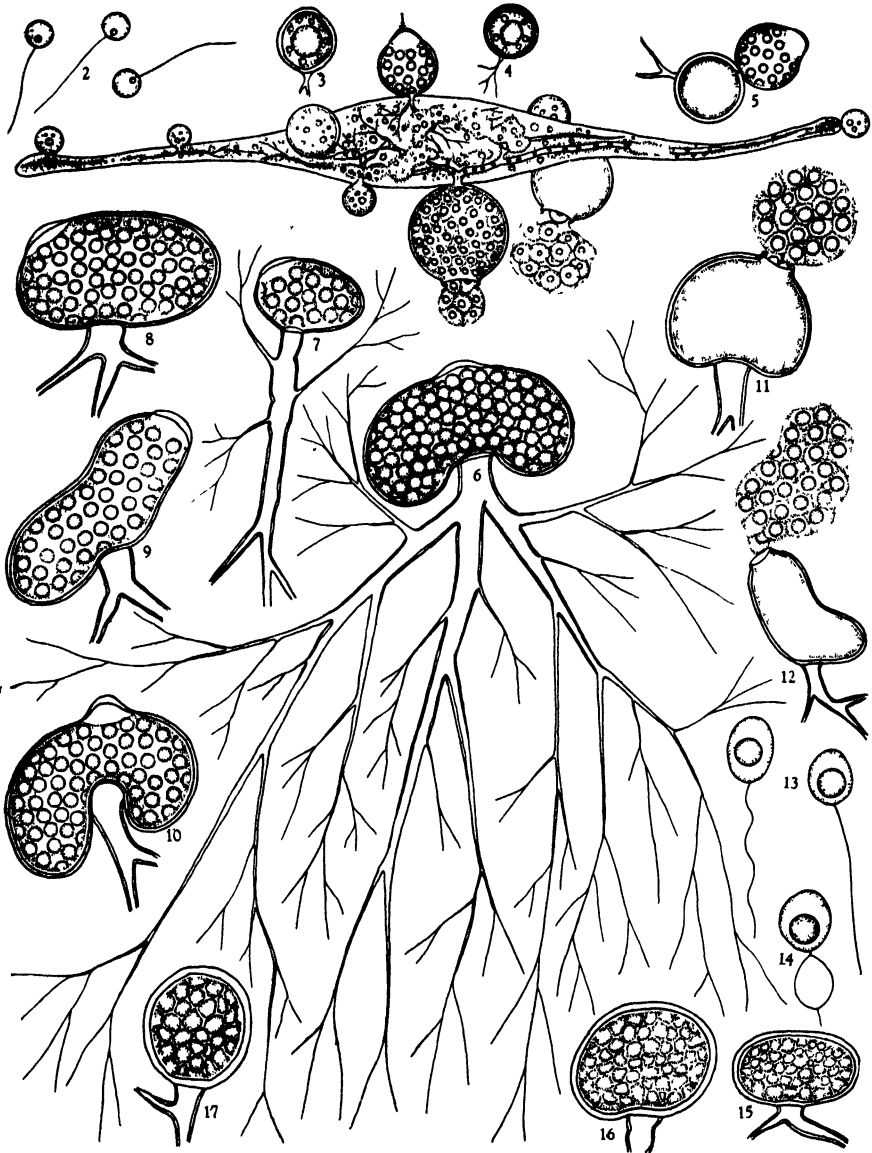
The sporangia may vary markedly in size and shape, but they are predominantly oval or elongated transversely to the main rhizoidal axis (figs. 7-9). They may also be almost hemispherical (fig. 11), reniform (fig. 6), or invaginated at the base (fig. 10), and nonapophysate.

Also, the rhizoids of this species are rather distinctive. They may branch frequently but not profusely, and appear to be very rigid and stiff (fig. 6) like those of *Rhizidium* species. Sometimes a large central axis with small side branches is developed (fig. 7), but in most thalli the main axis branches almost immediately beneath the sporangium (figs. 6, 8, 9). The main axes and branches may sometimes attain a diameter of  $12\ \mu$  and become thick-walled with age. So far no thalli have been found with rhizoids arising from several points on the surface of the sporangium as in species of *Rhizophlyctis* and *Karlingia*.

During dehiscence the operculum is pushed off and usually disappears quickly, but in rare instances it may persist at the edge of the exit orifice. The zoospores ooze out slowly in a globular mass (fig. 11), which soon becomes irregular in shape and floats away in much the same manner as in *C. appendiculatus* (fig. 12). Swarming of the zoospores in a vesicle outside of the sporangium has not been observed. The zoospores in the irregular mass appear to be stuck together and remain quiescent for 1-2 minutes, after which they begin to move about slowly and then swim away. In swimming they dart about unusually rapidly and change course abruptly. As the end of the motile period approaches, the zoospores swim round and round in circles which become progressively smaller. After the spores have come to rest, the flagellum may beat very rapidly without dislodging or moving the spore body. The flagellum appears to be unusually narrow or fine, and almost impossible to detect or see until the spores are completely at rest. A vesicle or vesicles may develop in it as it is gradually absorbed by the spore body (fig. 14).

The resting spores are oval (figs. 16, 17) to elongate or slightly flattened (fig. 15) like some of the sporangia, fairly thick-walled,  $1.5-2.3\ \mu$ , hyaline and smooth, and contain numerous angular refractive bodies which are usually closely packed together. The rhizoids on these spores are almost as extensive and thick-walled as those on the sporangial thalli.

**CHYTRIOMYCES FRUCTICOSUS.** This species grows well only on purified chitin and is, accordingly, chitinophilic. Its most striking characteristics are the bushy, bristly, and stiff-looking rhizoids which usually arise from

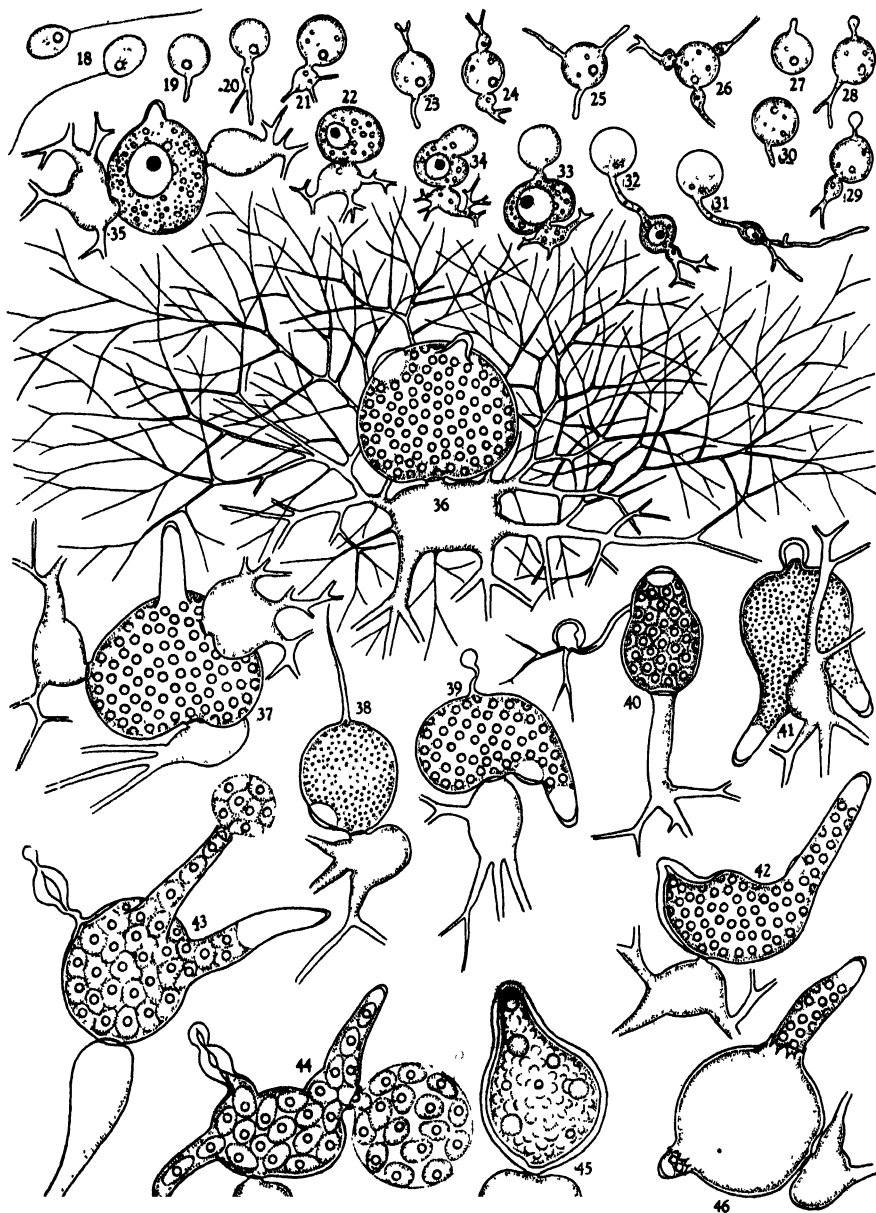


FIGS. 1-5. *Chytridiomyces Closterii*. FIG. 1. *Closterium rostratum* infected with 9 parasites in various stages of development and maturation.  $\times 1400$ . FIG. 2. Swimming zoospores.  $\times 1600$ . FIGS. 3, 4. Mature resting spores.  $\times 1400$ . FIG. 5. Germinating resting spore.  $\times 1400$ . FIGS. 6-17. *Chytridiomyces lucidus*. FIG. 6. Mature thallus with stiff, and rigid-looking rhizoids and reniform sporangium filled with large refringent globules.  $\times 1400$ . FIGS. 7-10. Variations in shapes and sizes of sporangia.  $\times 1400$ . FIG. 11. Dehiscent sporangium.  $\times 1400$ . FIG. 12. Discharged mass of zoospores floating away.  $\times 1400$ . FIG. 13. Swimming zoospores.  $\times 1700$ . FIG. 14. Zoospore with vesicle in flagellum.  $\times 1700$ . FIGS. 15-17. Variations in sizes and shapes of resting spores.  $\times 1400$ .

a large apophysis (fig. 36), and spiny to verrucose and echinulate, light- or greenish-brown resting spores. In these characteristics it resembles *C. stellatus* (Karling 1947a), but differs from this species by its smooth sporangia and distinctive resting spores. It also resembles *C. appendiculatus* by its thick-walled rhizoids and numerous appendiculate sporangia and resting spores. Another characteristic of *C. fruticosus* which has not been reported for other species of this genus is the development of a fairly large number of sporangia and resting spores from the germ tube instead of directly from the zoospore.

Accordingly, like species of *Karlingia* (Karling 1947b) and *Asterophlyctis* (Antikajian 1949), *C. fruticosus* has two types of development. The majority of sporangia and resting spores are formed directly from the zoospore (figs. 19-22), but out of 200 thalli studied 18 per cent of the sporangia and resting spores developed from the germ tube (figs. 30-33). These types of development are associated with and apparently determined by the position of the zoospore nucleus. If it remains in the zoospore, the latter develops into a sporangium or resting spore, but if it passes out into the germ tube during germination the sporangium or resting spore will develop at the place where it comes to rest. As in other species of *Chytriumyces*, *Asterophlyctis*, and *Obelidium*, the primary nucleus of the germinated zoospore, incipient sporangium, and resting spores is quite large and can be seen readily in living material (figs. 32-35). Therefore, its position in relation to the two types of development noted above can be observed easily under the oil immersion lens. In the less frequent type of development the passage of the nucleus into the germ tube and its space relation to the development of the sporangium or resting spore are fundamentally the same as those described by Antikajian (1949) for *Asterophlyctis sacpotoides* and need not be described here. Figure 40 shows an interesting sporangium with a zoospore cyst, and rhizoids attached by a germ tube. Apparently, in germinating the zoospore formed three basal germ tubes of which two developed into short rhizoids, while the third one gave rise to the sporangium after the zoospore nucleus had passed down into it.

Fairly often during germination the zoospore will form a short, broad germ tube or protuberance whose tip enlarges to become knob-like (figs. 27-29) and frequently has the appearance of a minute appressorium. Then at the opposite side of the zoospore another germ tube is formed which subsequently gives rise to an apophysis and rhizoids, or the sporangium or resting spore, depending on the type of development which is to follow. The formation of such appressoria-like structures during germination results eventually in knobbed sporangia or resting spores like those in figs. 39, 50, and 52. The wall of the knob and germ tube usually thickens con-



FIGS. 18-46. *Chytridiomyces fructicosus*. FIG. 18. Swimming zoospores.  $\times 1600$ . FIGS. 19-22. Germination and early developmental stages of mono-apophysate thalli.  $\times 1700$ . FIGS. 23, 24. Same for bi-apophysate thalli.  $\times 1700$ . FIGS. 25, 26. Same for tri-apophysate thalli.  $\times 1700$ . FIGS. 27-29. States in development of appressorium-like knobs on young thalli.  $\times 1700$ . FIGS. 30-32. Early stages of development of the sporangium from an enlargement of a long germ tube showing the nucleus in the enlarge-

siderably (figs. 43, 44) and in some cases they are solidly composed of wall material and very stiff or rigid looking.

As noted in the diagnosis above and shown in figures 35-39, the apophysis of this species is very large, conspicuous, and variable in shape. Some thalli may have two apophyses (fig. 35), and in rare cases three (fig. 37). They begin as local enlargements of the germ tube (figs. 20, 21), and in instances where the zoospore forms two or three germ tubes a similar number of apophyses may develop (figs. 23-26). Thus, at maturity they may be located at opposite sides or almost equidistant on the surface of the sporangium (fig. 35, 37) or resting spore.

A few nonapophysate thalli have been found with rhizoids arising at two or three points on the sporangium, and such thalli may be strikingly similar in appearance to *Karlingia* species. However, the two may be distinguished by the presence of a large primary nucleus in the fully formed sporangia of *C. fruticosus* (fig. 35), which apparently is lacking in *Karlingia*. As has been reported previously (Karling 1947a) for other species of *Chytriumyces*, division of the primary nucleus is delayed until the sporangia and resting spores have attained mature size. In *Karlingia*, on the other hand, it apparently divides very early in development because the fully formed sporangia are multinucleate.

The sporangia of *C. fruticosus* also vary markedly in size and shape (figs. 35-44), and instead of exit papillae they may develop long tubes. In some cases both papillae and tubes are formed on the same sporangium. The tubes may be up to 60  $\mu$  in length and usually taper markedly from base to tip. However, they do not always function in the discharge of zoospores and may remain closed at the tip. Occasionally, the operculum fails to develop at the tip and may form at the side or base of the tube (figs. 39, 42, 44). In anatrochous sporangia the necks may often extend down towards

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ment.  $\times 1700$ . FIG. 33. Same development from a short germ tube; nucleus clearly visible in incipient sporangium; zoospore case attached as an appendage.  $\times 1700$ . FIG. 34. Development of sporangium from only a portion of zoospore case.  $\times 1700$ . FIG. 35. Bi-apophysate, fully formed sporangium with large primary nucleus.  $\times 1400$ . FIG. 36. Portion of a mature thallus showing the characteristic stiff-looking, bushy rhizoids.  $\times 1400$ . FIG. 37. Tri-apophysate sporangium with short neck.  $\times 1400$ . FIG. 38. Sub-spherical sporangium with a terminal unbranched rhizoid and a basal exit papilla.  $\times 1400$ . FIG. 39. Knobbed, anatrochous sporangium with short neck and basal exit papilla.  $\times 1400$ . FIG. 40. Stalked non-apophysate sporangium which apparently developed from the germ tube; zoospore case with rhizoids attached at left.  $\times 1400$ . FIG. 41. Appendiculate sporangium with two necks extending down towards apophysis.  $\times 1400$ . FIG. 42. Sporangium with wall thickened at one end.  $\times 1400$ . FIG. 43. Discharge of zoospores from a sporangium with two necks; appressorium-like knob and zoospore case attached at left.  $\times 1200$ . FIG. 44. Zoospores swarming in a vesicle; exit tubes or necks non-functional.  $\times 1200$ . FIG. 45. Dormant, thick-walled sporangium.  $\times 1200$ . FIG. 46. "Germination" of thick-walled sporangium.  $\times 1200$ .

the apophysis (figs. 39, 41). Sometimes the sporangia may become thick-walled and light brown in color and go into a dormant state as in *C. appendiculatus* (fig. 45). Then, when they form zoospores the exit papillae or tubes break through the thick wall (fig. 46).

During dehiscence the operculum is pushed off by the emerging zoospores and disappears quickly from view. The mass of zoospores is surrounded by a layer of matrix which expands as more and more spores are discharged. In a short time a delicate vesicle is formed in which the zoospores swarm actively for 1-2 minutes (fig. 44). When the vesicle ruptures, the zoospores dart out, but usually they do not swim far away. Instead, they frequently come to rest in groups and germinate, which results in the development of aggregates of sporangia or resting spores on the chitinous substratum. Germination of zoospores in situ occurs occasionally with the result that either sporangia or resting spores may develop within the old sporangium.

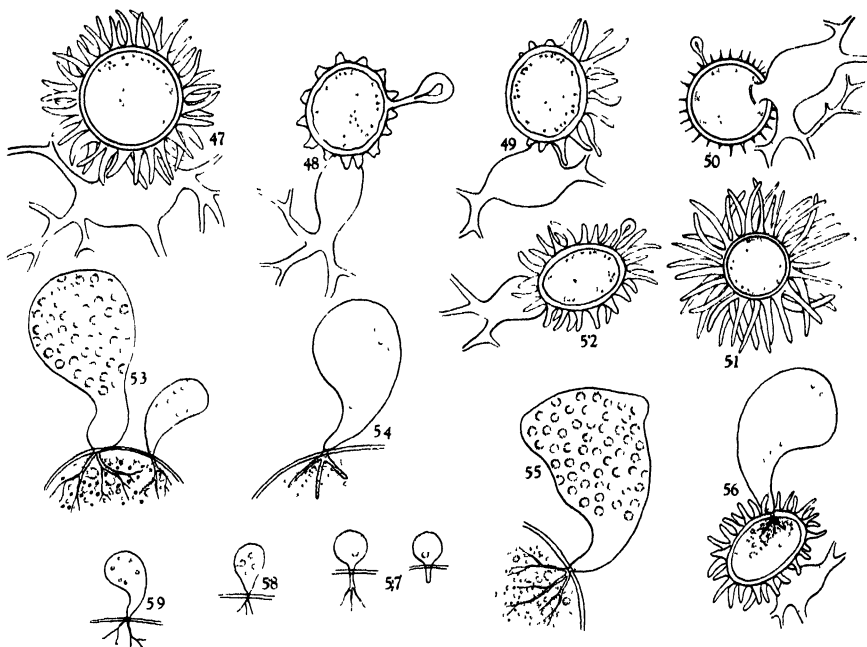
The resting spores develop directly from the zoospore (figs. 47, 49-52) or from an enlargement of the germ tube in the same manner as the sporangia described previously. In the latter type of development the empty zoospore cyst and germ tube may persist as an appendage to the spore (fig. 48) and usually become thick-walled. They frequently look like the male thallus and conjugation tube or canal which are attached to the resting spore of *Siphonaria*. Therefore, unless the developmental stages are studied carefully one might conclude that such resting spores in *C. fructicosus* have developed as the result of fusion of two thalli. The development of these spores is fundamentally similar to that described by Antikajian for *Asterophlyctis sarcoptoides*.

The spines or conical pegs on the spores vary from 22 to 70 per spore, taper gradually and may be up to  $15\ \mu$  long in exceptional cases (fig. 51). The usual length is between 4 and  $8\ \mu$ , with a width of  $2.5-3.5\ \mu$  at the base. On some spores they may be reduced to warts (fig. 48) so that such spores are distinctly verrucose. Figure 49 shows an exceptional spore which is partly smooth, verrucose and spiny. Echinulate spores are rare (fig. 50) and so far no completely smooth ones have been found.

PARASITE OF *C. FRUCTICOSUS*. During the course of this study the sporangia and resting spores of *C. fructicosus* became parasitized by another small chytrid which possibly belongs in the genus *Rhizophydium*. Its sporangia are broadly obpyriform or clavate,  $15-22 \times 24-30\ \mu$ , with a tapering, curved base (figs. 54-56). The sporangia are quite broad at the apex, and in some cases they may be almost flat on top (fig. 55). The apical exit papillae are not prominent or conspicuous, and so far I have been unable to determine whether or not the sporangia are operculate. The rhizoids are intramatrical and branched, fairly short and broad in diameter, and

sometimes abruptly tapered. In a few sporangia observed, the rhizoids were reduced to digitate structures (fig. 54).

Whether or not this chytrid is an obligate parasite of *C. fructicosus* is not certain, but it may be noted here that it did not parasitize *Cladochytrium replicatum*, *Nowakowskiella macrospora*, *N. profusa*, *Chytridiomyces hyalinus*, *Aphanomyces laevis*, and *Pythium* sp., which were growing in the same culture. In one instance it was found parasitizing the main rhizoidal



FIGS. 47-52. *Chytridiomyces fructicosus*. FIG. 47. Large spherical resting spores with long tapering pegs or spines.  $\times 1400$ . FIG. 48. Verrucose resting spore with zoospore case and germ tube at right.  $\times 1400$ . FIG. 49. Partly smooth, verrucose and spiny resting spore.  $\times 1400$ . FIG. 50. Echinulate spore with knob.  $\times 1400$ . FIG. 51. Small spherical spore with unusually long spines.  $\times 1400$ . FIG. 52. Knobbed, oval resting spore.  $\times 1400$ . FIGS. 53-59. *Rhizophyidium*-like parasite of *C. fructicosus*. FIG. 53. Mature and young sporangia with branched rhizoids.  $\times 1400$ . FIG. 54. Curved sporangium with digitate rhizoids.  $\times 1400$ . FIG. 55. Mature sporangium with flattened top.  $\times 1200$ . FIG. 56. Parasitized resting spore of *C. fructicosus*.  $\times 1400$ . FIGS. 57-59. Germination of zoospore and early developmental stages of thalli.  $\times 1600$ .

axis of *C. fructicosus* where it caused a distinct enlargement or malformation. However, no malformations were noted in cases of infected sporangia. In such structures part of the protoplasm accumulates around the rhizoids of the parasite, while the remainder undergoes degeneration.

No resting spores of the parasite were observed. Therefore, it is impossible to classify or properly name this chytrid at present. Nevertheless, it should be noted here that its sporangia are somewhat similar in shape to



those of *Phlyctidium mycetophagum* (Karling 1946b) which parasitizes *Chytriomyces hyalinus*, *C. aureus*, and *C. appendiculatus* among numerous other chytrids. In the latter parasite, however, the rhizoid is unbranched and usually thread-like or filamentous, and the two species differ in this respect. The parasite of *C. fruticosus* is probably a member of *Rhizophydium* which includes parasites of *Chytriomyces* and other chytrid genera (Karling 1946a, c), but its identity will remain uncertain until its resting spores have been found and the presence or absence of an operculum has been definitely established.

Besides the three new species of *Chytriomyces* described above, *C. hyalinus*, *C. aureus*, *C. appendiculatus*, *C. stellatus*, and *C. spinosus* were isolated on cellulosic and chitinous substrata from soil and water collected in various parts of Maryland. Species of this genus are accordingly well represented in the soil flora of Maryland.

With the addition of these new members, the genus *Chytriomyces* includes at present ten species, one of which *C. nodulatus*, is of questionable validity in the author's opinion. Of these ten species, two are parasitic on fungi and algae, and the remainder are saprophytes.

#### SUMMARY

Three new species of *Chytriomyces*, *C. Closterii*, *C. lucidus*, and *C. fruticosus* were found in fresh-water and soil in various parts in Maryland. *Chytriomyces Closterii* parasitizes *Closterium rostratum* and appears to be limited in host range to this alga. It is distinguishable by small spherical or broadly pyriform sporangia, minute zoospores, and spherical, hyaline resting spores.

The other two species are saprophytes and were isolated from soil and water on cellulosic and chitinic substrata. *Chytriomyces lucidus* is characterized primarily by large zoospores with an unusually large refractive globule which gives them and the sporangia a glistening appearance, and by stiff-looking and bristly rhizoids, and hyaline, smooth resting spores. It was isolated and growing on bits of onion skin, and does not grow on chitinous substrata. In contrast, *C. fruticosus* is chitinophilic in relation to its substrata. It is distinguishable by its bushy rhizoids which arise from one or more apophyses, appendiculate sporangia, and spiny, greenish-brown resting spores. It was often found to be parasitized by another *Rhizophydium*-like chytrid.

In addition to these new species of *Chytriomyces*, *C. hyalinus*, *C. aureus*, *C. appendiculatus*, *C. spinosus*, and *C. stellatus* were isolated from soil and water in various parts of Maryland.

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## TORREY BOTANICAL CLUB

A luncheon meeting of the Torrey Botanical Club is to be held on Thursday, December 29th, at the Hotel McAlpin, in connection with the New York meeting of the A.A.A.S. Dr. W. H. Camp will be the speaker. Tickets will be available at the supplementary registration desk of the A.A.A.S. in the Hotel McAlpin.

Parlor B on the Mezzanine of the Hotel McAlpin will serve as headquarters for the Torrey Botanical Club throughout the week of meetings.

## TORREYA

## PROCEEDINGS OF THE CLUB

**Minutes of the meeting of February 1, 1949.** The meeting was called to order at 8:05 P. M. by President Matzke at Columbia University; 51 members and friends were present. Dr. B. O. Dodge of the N.Y.B.G. spoke on "Taxonomic and genetic features bearing on the origin of *Neurospora tetrasperma*." Dr. Dodge's abstract follows:

The genus *Neurospora* was proposed by Shear & Dodge to include those species of the Sphaeriales having dark striated ascospores and orange-colored conidia borne on dichotomously branched sporophores. The perfect stage of the well-known bakery mold, or red bread mold, was named the type species. It appears that this mold was first mentioned in scientific literature in 1843, when Léveillé referred to it as *Oidium aurantiacum*; that same year Montagne described and illustrated it under the name *Penicillium sitophilum*. The authors of the new genus *Neurospora* discussed the systematic relations of the bakery mold to other Sphaeriales, but were unable to suggest whence it arose. As is to be expected, the fungus has been described under a number of different names; it appears that *N. sitophila* is the correct one.

There are six species of *Neurospora*, three of which have 8-spored asci; they differ in the dimensions of asci and ascospores. *N. crassa* seems to have somewhat smaller conidia, which are more pinkish in mass than those of other species. The other three *Neurosporas* have 4-spored asci which clearly differ in morphology. *N. Toroi* and *N. tetrasperma*, although they differ morphologically only slightly, cannot readily hybridize. While the accumulation of very small changes in an 8-spored species may have given rise to the first 4-spored one, such a type could have arisen suddenly by way of few macromutations; it seems unlikely that the first 4-spored species was ancestral to the others. Regardless of the manner of origin of species—whether by slight or large mutations—it seems certain that the 8-spored are ancestral to the 4-spored.

Evidence has accumulated suggesting that *N. tetrasperma* may have arisen directly from the *N. sitophila* type, even though these species differ in other respects than the number of spores. Asci of *N. tetrasperma* sometimes contain five spores, two smaller than the rest, and of the same size as those of *N. sitophila*. The small spores are so often at the lower, somewhat narrower end of the ascus that it seems likely that with reduction in diameter of the whole ascus the species would revert to 8-sporedness, or conversely that 4-sporedness may have become established in an originally 8-spored species as a result of broadening and shortening of the ascus.

Some ten years ago the discovery was reported of a heterocaryotic race of *N. tetrasperma* in which nuclei of one mating type carry a lethal gene, those of opposite type being normal. This lethal has three distinct effects: 1. On corn-meal agar the heterozygous *E/e* asci usually aborted without delimiting spores. 2. In the occasional instances when the lethal did not cause abortion the asci produced eight small spores instead of the four large ones characteristic of the species; the small spores were indistinguishable from those of *N. sitophila*. 3. The lethal factor was shown to be in-

herited according to a simple Mendelian ratio: four of the ascospores carried a single *E* nucleus, and four the normal *e*. Those carrying the lethal *E* often germinated but on corn-meal agar soon died; the other four developed normally. An occasional ascus was 7-spored; the giant spore was heterocaryotic for mating-type and for the lethal. By propagating vegetatively by transplantation the original heterocaryon has been preserved for 10 years. By propagating from the large spores it was possible to carry the lethal from generation to generation through the sexual phase of reproduction; from the small normal *e* spores came only the normal *N. tetrasperma* with four large spores.

The reversion from the 4-spored to the 8-spored type was then only a temporary one; at the first opportunity the lethal is eliminated. Recent work has been directed to the problem of carrying the lethal through to growth into functional mycelia. By plating out the conidia from heterocaryotic (*E/e*) mycelium and selecting the smallest and most abnormal germinating conidia for transfer to a special agar, several races pure for the lethal were obtained. The culture medium was a potato-dextrose agar in which the potato decoction was made from new or half-grown potatoes. It was of course necessary to test the isolates for purity. Several of the mycelium gave rise to 8-spored asci, and were therefore shown to carry *E*.

The new-potato-steep dextrose medium which was potent to prevent ascus abortion was found to be potent to a certain extent to prevent the death of ascospore germings. In this way it has been possible to obtain 31 races pure homocaryotic for the dominant lethal *E* which will grow and function in sexual reproduction when mated with normal *e* tester races of *N. tetrasperma*.

The next step is to obtain races of both mating types carrying the lethal *E*. From such races could be obtained asci homozygous for *E*, and ascospores all carrying the lethal. Along with the strain of opposite mating-type must be discovered an agar on which the life cycle can be carried to completion. The reversion from 4-sporedness in *N. tetrasperma* will then be permanent. The resulting fungus will still not be *N. sitophila*, since the species differ in other characters. But in the most significant respect, spore-number, the first step in permanent reversion has been accomplished.

After lively discussion of the address, the meeting was adjourned at 9:25.

**Minutes of the meeting of March 16, 1949.** After refreshments served by members of the University, the meeting was called to order at 4 P.M. by President Matzke at Fordham University; 58 members and friends were present. The minutes of the preceding meeting were read and approved. Dr. Charles Berger spoke on "Recent botanical research at Fordham." Dr. Berger's abstract of his address follows:

Another case of the natural occurrence of polyploid cells in the development of a diploid plant has been found in the silk tree, *Albizia julibrissin*. Several interesting differences between the phenomenon as it occurs in *Albizia* and in two previously reported cases were described.

A new case of endomitosis in the tapetal cells of the snapdragon *Antirrhinum majus* was also reported. Some of the tapetal cells undergo two successive endomitotic divisions which may be followed by a normal mitotic division of the polyploid cells.

Afterwards time-lapse phase-contrast microcinematographs were shown of the process of meiosis. No further business was transacted. The meeting was adjourned at 5:10.

**Minutes of the meeting of April 5, 1949.** The meeting was called to order at 8:10 P. M. by President Matzke at Columbia University; 37 members and friends were present. The minutes of the preceding meeting were read and approved.

The following names were presented for election to membership: **Life Member:** L. J. Gier, Liberty, Mo. **Active Members:** Mrs. Gily E. Bard, New Brunswick, N. J.; Clarke Q. Brown, Caldwell, Idaho; Percy Camp, Toms River, N. J.; Mrs. Percy Camp, Toms River, N. J.; Allan P. Chan, Ottawa, Canada; Mavin S. Dunn, Lansdowne, Pa.; Robert C. Frohling, Union, N. J.; A. S. Heiba, Tucson, Ariz.; Doris Holtzman, Brooklyn, N. Y.; Jeanette M. Dryn, Buffalo, N. Y.; Jose V. C. Malato Beliz, Elvas, Portugal; Harold McIlvaine, Moscow, Idaho; Marion R. Myles, Nashville, Tenn.; Lindsay S. Olive, New York, N. Y.; Elsie Phelon Phillips, New York, N. Y.; Harry K. Phinney, Corvallis, Ore.; H. W. Popp, State College, Pa.; W. C. Price, Pittsburgh, Pa.; B. A. Razi, Bangalore, India; Donald D. Ritchie, New York, N. Y.; S. B. Shively, Lincoln, Nebr.; Edward E. Terrell, Ithaca, N. Y.; Sylvia White, Washington, D. C.; John L. Wood, Mont Alto, Pa. **Associate Members:** Charles Bell, Lower Bank, N. J.; Marie E. Boyle, Bryn Mawr, Pa.; Harold E. Clark, New Brunswick, N. J.; Ruth Goodman, New York, N. Y.; Richard D. Ilnicki, Jamesburg, N. J.; William P. Jacobs, Princeton, N. J.; Gordon N. Murray, Martin, Tenn.; Kathleen Prestwidge, New York, N. Y.; Anne O. Seaman, New York, N. Y. All were elected.

Dr. Zimmerman announced, for the committee to find a successor to Dr. Rickett as editor of the Bulletin, that Dr. Rickett's resignation had been accepted and Fr. Berger elected to that post by the Council. It was unanimously voted that the thanks of the Club be extended to Dr. Harold Rickett for his long, faithful, and successful service as editor.

The committee for the Andrews Research Fund reported that the following grants for research had been made from the Fund: Dr. Richard Goodwin, \$300; Dr. Robert Clausen, \$250; Brother Leon, \$150; Dr. Charles Heimsch, \$250.

Dr. Richard Goodwin of Connecticut College discussed his "Studies on the fluorescence of roots." His abstract follows:

The tissues of plants when placed in ultraviolet light are likely to exhibit fluorescence as a result of the presence of fluorescing organic compounds within the cells. Green tissues exhibit a red chlorophyll fluorescence which is so bright that the fluorescence of other compounds is likely to become obscured. The fluorescence of these other compounds can be observed more clearly in non-green organs such as roots.

The speaker wishes to acknowledge the collaboration of Dr. Frederick Kavanagh in the work which is being reported. The roots of 135 species of vascular plants, representing 69 families, have been examined in ultraviolet light. Of these, all but six species of ferns with much dark pigment in the roots exhibited fluorescence. The color of the fluorescence was most frequently blue, bluish, or bluish-white, but was sometimes greenish, greenish-yellow, or red. The fluorescing substances have been extracted with acetone and with n-butanol from the roots of nine different species, including three of the above-mentioned ferns. The blue-fluorescing material extracted from *Avena sativa* roots has been separated into at least three distinct fractions which can be distinguished by their partition between immiscible solvents, by their adsorption on chromatographic columns, and by the intensity of their fluorescence over a wide range of acidity.

One of these fractions has been identified as the coumarin derivative scopoletin, by comparing the pH-fluorescence curve and the ultraviolet ab-

sorption spectrum of the extract with that of a pure sample of scopoletin. Scopoletin is present in the mature portions of five-day-old *Avena* roots in concentrations in excess of  $5 \times 10^{-5}$  molar. From 3 to 18 mm. behind the root apex the amount of scopoletin was found to lie between 0.75 and  $1.5 \times 10^{-9}$  g., while in the apical 3 mm., which includes the meristem and region of cell elongation, the amount was too small to measure but was certainly less than  $0.08 \times 10^{-9}$  g. Recent studies have shown that coumarin derivatives and other compounds having an unsaturated lactone structure have growth-inhibiting properties, and it has recently been suggested that this may be tied in with the inactivation of sulfhydryl-containing enzymes. Whether scopoletin acts as a natural growth regulator is not known, but the fact that it is present in mature portions of *Avena* roots at concentrations high enough to inhibit growth while it is practically absent from the growing tip is suggestive.

After discussion the meeting was adjourned at 9:30.

Respectfully submitted,  
DONALD P. ROGERS,  
Recording Secretary.

#### FIELD TRIP REPORTS

**April 3, 1949. The Pine Barrens and Plains of New Jersey.** The main purpose of the trip was to view the broom crowberry (*Corema Conradii*) in flower. The season being somewhat advanced, only scattered blossoms remained. The station near Sim's Place was still healthy and vigorous. It is safe to say that on the West Plains acres of the crowberry are in good condition. The trailing arbutus (*Epigaea repens*), pyxie moss (*Pyxidanthera barbulata*), and sand myrtle (*Dendrium buxifolium*) were in bloom on the Plains and even a few early blossoms of the pine barren heather (*Hudsonia ericoides*) appeared.

**April 14-16. Knoxville, Tennessee.** Apparently no Torreyites attended the Knoxville meeting. At least no reports have reached the field chairman.

**April 17. Pelham Bay Park, New York City.** The group left for the Park at 10:15 A.M. The weather was clear but with a cool wind blowing. Very few spring flowers were noted and the marine flora does not usually appear until late spring. At the start of the trip the following marine algae were seen: *Enteromorpha intestinalis*, *E. Linza*, *Asperococcus echinatus*, *Fucus vesiculosus*, *Ulva lactuca*, and at least two species of *Poly-siphonia*. Other marine algae were noted but not identified. A rather rare shrub, *Amelanchier oblongifolia* var. *micropetala*, a dwarf junberry, was observed coming into leaf where growing in crevices of rocks on the shore at the northern part of the Park. Attendance 10. Leader, William Rissanen.

**April 17. Farmingdale, N. J.** Eight members reported for this trip and as there were five cars we could have welcomed members by train. A walk along the railroad showed several plants though nothing startling but the river bottom along the Manasquan was yellow with *Caltha*. We seemed to disturb the trout fishermen there.

In the park area at Allaire, *Dicentra Cucullaria* had not yet reached its prime but many blossoms were out. *Viola scabruscula* was abundant.

We visited the old ruins and found many cars there before us. Public interest seems to have awakened in the new state park. It is to be hoped that the flora does not suffer its usual fate in parks. Leader, Vernon L. Frazee.

**April 24. Lakehurst, N. J.** Rain failed to dampen the spirits of the group that assembled at the railroad station, and the Torrey group was soon joined by two carloads

of students and professors from Bucknell University, who were on the last lap of a four-day field trip.

The single bald cypress (*Taxodium distichum*) that persists at Lakehurst was visited first. High-bush blueberry (*Vaccinium corymbosum*) was flowering in abundance, as was pyxie moss (*Pyxidanthera barbulata*), sand myrtle (*Dendrium buxifolium*), shadbush (*Amelanchier canadensis*), black chokeberry (*Aronia nigra*), and bird-foot violet (*Viola pedata* var. *lineariloba*). Although Lake Haricon at Lakehurst was being cleaned up a bit and most of the water drained off, the golden club (*Orontium aquaticum*) was everywhere in the upper stretches of mud covered lake bottom. The lance-leaved white violet (*Viola lanceolata*) grew along the shores and tiny, newly-formed leaves of the three species of sundews were just unfolding. Buds of the pitcher plant (*Sarracenia purpurea*) were beginning to form. Forays to nearby areas yielded several additional species. Ridge-way produced beautiful pink blossoms of the trailing arbutus (*Epigaea repens*); Colliers' Mills, the field pansy (*Viola Rafinesquii*); and Van Hiseville, budding blue lupine (*Lupinus perennis*). The highlight of the day came at its close. The members and guests remaining at dusk were shown the breath-taking beautiful swamp pink (*Helonias bullata*) near Allaire by Mr. Vernon Frazee who had known of the station since his youth. It left a very pleasant and lasting impression upon those viewing it for the first time. Attendance 20. Leader, David Fables.

**April 30. Inwood Hill Park, N. Y.** Ten Torrey members and guests joined in the botanical trip to Inwood Hill Park in the northwestern corner of Manhattan Island.

J. K. Small, in an article entitled "The Jungles of Manhattan Island—II" (Jour. N. Y. Bot. Gard. 38: 308-316. 1937) listed the trees and shrubs of the area. A careful survey of Inwood Hill would certainly discover many additional species not noted by Small. These might serve as the subject of a short supplement, which would be not only interesting in itself but also, in a retroactive way, enhance the value of Small's census. For instance, the deerberry and the lowbush blueberry were listed by Small, but not *Vaccinium corymbosum* and *V. atrococcum* observed by the group. On the top of a hill was seen *Lyonia mariana*, which the writer first noticed there in 1936. Small listed the flowering dogwood, but missed *Cornus racemosa* (*C. paniculata*). We stopped to examine this species because of its peculiar leaf-scars which are deciduous in the springtime like those of *Hamamelis*. *Cornus rugosa* (*C. circinata*) is quite rare in the area, and Small's oversight of it is understandable. We suspect that the introduction into Inwood Hill Park of *Rubus phoenicolasius* and *Ribes sativum* (the common *R. vulgare* of manual, the anther-sacs being separated by a broad connective) must have antedated Small's study, but these two were missed.

Small's paper dealt with only the woody plants. It should be profitable to publish on the herbaceous flora of Inwood Hill Park. This park and Fort Washington Park are the only two remaining wild areas of appreciable size in Manhattan, and a complete list of their plants would have historical interest not far in the future.

The Torrey Botanical Club noticed quite a number of flowers on the April 30th trip. Especially attractive were large colonies of *Dentaria diphylla* and *Althaea officinalis*. On the east face of an old stone wall grew a beautiful cover of *Linaria cymbalaria*. The writer has seen the kenilworth ivy on the same mossy wall since at least 1933, the same miniature violet dragonheads, two yellow spotted in front and sharp spurred behind. A close group of *Podophyllum peltatum* formed a low continuous canopy of shield-shaped leaves, which when lifted revealed the large white waxy flowers, nodding and richly fragrant. In the center of each blossom sat the plump pistil capped with its thick intricately undulate stigma; beneath, the pedicel showed minute streaks of ruby. The number of stamens varied. According to the Manual the number of stamens should be twice the number of petals. In two flowers bearing 6 petals we counted 10 stamens, one being very much reduced, and 17 stamens, four being much reduced.

Another interesting observation for the Torrey group was the seedling habit of *Acer pseudoplatanus*. Notwithstanding its dicotyledonous classification, specimens were ob-

served with three and four cotyledon-leaves in a whorl, and sometimes two with one deeply cleft. Judging from the nervature, the bilobed form is apparently best interpreted as two partly united cotyledons.

On the way out of the park, near the end of our trip, we saw along the walk a plantation of *Quercus ilicifolia*. The many dangling catkins presented an unusual and especially charming effect, being almost at eye level because of the scrub habit of the oaks.

It is recommended that the trip be repeated next year and a detailed list be kept of the species seen. Leader, Joseph Monachino.

**May 20-22. Branchville, N. J.** The thirty-fifth annual nature conference was held as scheduled. All but one of these sessions have been held at Branchville. During wartime restrictions on travel the Summit Nature Club took us to Watchung Reservation for the conference in 1945. For three seasons, during a change of management at The Pines, we were guests at The Haltere Hotel on Culvers Lake and this year an overflow of thirty-five participants were quartered there. A very interesting geology tour of Sussex County included outcroppings of rocks of various ages. An old rock (Oriskany limestone) but a recent habitation (Indian shelter) was seen at Bevans. This has been rereproduced as a habitat group in the State Museum at Trenton. A botanical excursion was made to Tillman Ravine in Stokes Forest and much botanizing was done around the hotel. Several species were added to the permanent list of plants: *Peziza* sp., *Fissidens* sp., *Adlumia fungosa*, *Angelica atropurpurea*, *Gaylussacia baccata* (thought to be a correction of the previously reported *G. dumosa*), and *Thalesia uniflora* (*Orobanch* in Gray's Manual). A large quantity of *Marsilea quadrifolia* was found on the small lake back of the hotel. This apparently brings to 617 the number of complete identifications from the region. This list, corrected to 1948 may be obtained from Dr. H. N. Moldenke, New York Botanical Garden. The bird list ran to 105 species. Evening lectures on the above subjects were held as usual. Attendance, 123, from 5 states. Leaders: David Fables, Louis Hand, James Hawley, Henry Herpers, Jr., Wallace Husk, Mr. and Mrs. C. B. Schaughency, Edgar T. Wherry.

#### REVIEW AND DISCUSSION

**Introggressive Hybridization.** By Edgar Anderson. ix + 109 pages. *Pl.* 1-5; *fig.* 1-23. John Wiley & Sons, New York. 1949. \$3.00.

Within the next year biologists will be celebrating the semicentennial anniversary of the rediscovery of Mendel's laws of inheritance. Yet, during this half-century of rapid advance in our knowledge of inheritance in living things, taxonomy in general has remained aloof from genetic concepts. For the most part its devotees have proceeded as if genetic phenomena were not present "in nature" but occurred only under the so-called controlled conditions of the breeder. Dr. Anderson's little book should go far in dispelling this common misconception regarding one facet of our knowledge concerning the genetic structure of the natural population.

The great multiplication of infraspecific names within recent years is clear evidence that taxonomists are beginning to discover the variability so characteristic of many of the taxa designated by them as species. Perhaps out of modesty the originator of the term "Introggressive Hybridization" has refrained from pointing out too forcibly that, to a large extent, this common phenomenon is the cause of much of the complexity which is confounding classical taxonomists and driving them to excessive nomenclatural tinkering.

The fact of widespread introggressive hybridization and consequent gene flow must be faced by the taxonomist if he is to bring to his studies any semblance of reality. The futility of attempting to jam the wide variability of such populations into relatively few named categories, or the equal absurdity of attempting to be logical and give all the variants "adequate" nomenclatural treatment by the recognition of a large series of named taxa, is amply shown by the examples given. At no place has the author crossed swords with the classical taxonomists having, instead, merely analyzed the various



examples; in less patient hands they might easily have been bludgeoned over the head with what to them must surely be bitter facts.

The author tells us what genic introgression is, how it is initiated, how it operates, and what its results may be; he even presents us with an interesting and lucid chapter on various special techniques for studying and measuring it. But, as a geneticist, he has wisely refrained from recommending how such situations are to be handled nomenclaturally.

It appears quite probable, if one may look ahead, that in the not-too-distant future the present classical hierarchy of "species, subspecies, variety, and form" will be found inadequate to express with any real precision the spread of variability which is present in nature, and that a totally new system will have to be devised. What form this new nomenclatural system will take not even this reviewer is sufficiently rash to predict. However, if taxonomists are to continue naming organisms some functionally workable system must be devised to take proper care of the biologically important and ubiquitous phenomenon of introgressive hybridization. It is a responsibility which the taxonomist dare not evade, lest he become a dilettante member of the body biologic.

The text of this small volume is easy to read, being without the mass of interpolated (and perhaps necessary) mathematical formulae characteristic of so many present-day advanced works on population genetics. However, the mathematics of a naturally segregating population always is there, bolstering the background of the account, but never intruding sufficiently to obscure the fundamental picture of the broader aspects and implications of the situation. Therefore the busy herbarium taxonomist can offer no excuse for not reading this brief and lucidly written work. Furthermore, if he is honestly conscientious, he may be brought to ask himself just what sort of botanical data he is gathering when he hurriedly snatches a single specimen from a large and often variable local population.

The author clearly indicates that he is not dealing with such phenomena as apomixis and polyploidy; they are outside the scope of this monograph. However, the reader should disabuse himself of any idea he might have that polyploids cannot be afflicted with introgressive hybridization. To one who has to be continually dealing with such things, it is obvious throughout much of the text that the author is outlining the genetics of diploid populations. What Dr. Anderson has to say about the inherent and actual complexity of an introgressively hybridized population on the diploid level would be increased in geometric progression were he to have taken his readers through the various polyploid levels as well. Fortunately for the classical taxonomist who perhaps might be easily scared with para-astronomical numbers, as yet no precise analytical data are available regarding such populations. But the potentialities should be kept in mind by those dealing with polyploidally complicated groups.

Because of space limitations the author has had no opportunity to venture down some of the interesting byways of the problem. One of the most disconcerting things for a student is to discover that what he supposed to be only a case of introgressive hybridization actually is an instance of a segregative allopolyploid, perhaps superposed in nature on a case of true introgression on the diploid level. The close series of apparent "hybrid intergrades" found where the species involved already are polyploid and have a still higher allopolyploid population superposed on them is, to say the least, somewhat confusing to the student beginning a population analysis. Having fallen into this botanical booby-trap on various occasions in the past, this reviewer knows how embarrassing it can be. There is no way yet known to be reasonably certain of avoiding this error except by making a rapid cyto-reconnaissance of the material. If the group under scrutiny proves to be homoploid then Dr. Anderson's methods for the detection and analysis of introgressive hybridization will be effective and revealing. On the other hand, if a sampling of the group indicates the presence of a heteroploid condition, then quite a different series of analytical techniques will have to be brought to bear on the problem before it can be satisfactorily clarified.

There are several other places where this reviewer could wish that the author might have had opportunity to expand the text. One of these is in Chapter 4 where it is postu-

lated that, in a segregative population, the extreme homozygous types would tend to increase in frequency in succeeding generations, "the exact results depending on the natural mating system, the size of the populations, etc." It is hoped that "etc." covers such things as sterility factors for, in general, these tend to accumulate with the advent of homozygosity; therefore, population segments with such genetically determined sterility factors—and additional examples are being discovered all the time—usually trend more toward the heterozygous than the homozygous condition. Linkages and the "recombination spindle" admittedly do tend to keep the bulk of a segregating population within certain bounds; even so, evolution does not proceed with the norm but with the exceptional, and selective forces surely will accentuate fortuitous nodes of accumulation on the over-all gene pattern.

There is, however, one theme running through the book with which this reviewer would take issue. This is neither a criticism of material nor of interpretation but, rather, one of a repeated implication which is bound to crystallize the reader's attention on special events, leading to a possible conclusion that introgressive hybridization is a rare and transitory phenomenon of no great importance in the broader interpretations of general systematics. Certainly the author does not say this; in fact he cautions that it is otherwise. Yet the implications from the various examples given might lead the casual reader who has done no work in genetically introgressive populations to regard the phenomenon as of sporadic occurrence. For example, on page 13 one reads that "it is only where man or catastrophic forces have 'hybridized the habitat' that any appreciable number of segregates survives"; man as the primary disturbing agent in restricted areas is the recurrent theme in Chapter 1; on page 62 we read again of "Floods, fires, tornadoes, and hurricanes" and on page 63, in times of flood "Trees are undermined and swept away; . . . plants are transported bodily"; etc., as if these were the sole factors initiating introgressive hybridization. Now this reviewer certainly does not discount them as important factors; they are real and potent. Furthermore, they are about us every day and we can easily see them in action, note their immediate effects, and observe the results on the populations moving into these catastrophically affected but often relatively restricted areas, especially since they are easily encompassed by the individual student. Yet, important as they are, they are not the only factors—perhaps not even the most important factors—upon which we should keep our eyes and attention focused. Quite often their best function is served by providing restricted areas wherein may be observed, in miniature, something similar to the development of the great genic complexes of the past out of which our present floras have developed.

On page 65 the author admits that it is "probable" that Pleistocene conditions may have had much the same effect as these lesser phenomena, and that the eastward extension of the grasslands in post-Pleistocene time also may have been an important factor in setting the stage for introgressive hybridizations in many groups. Although the advances of the Pleistocene ice-fronts certainly were catastrophic, their retreats scarcely should be classed as such—and it was during the retreats that the many new habitats were laid open for occupancy by the introgressants with their various genic combinations. The factors causing the eastward advance of the grasslands, an event that probably was initiated in the present Sonoran region as early as the Miocene and which reached its eastward maximum no more than 6,000 years ago, certainly had a deleterious effect on the forests of a wide area during the long period of that great floristic migration, but it is doubted that the movement should be thought of as coming under the heading of sudden catastrophe; certainly it would not be of the same order as a local flood, a fire or tornado.

The fluctuations and ultimate emergence of the southeastern Atlantic and Gulf coasts of America throughout the Tertiary yielded a series of different, intergrading and constantly changing habitats; earth-movements and not man initiated the changes, and they were neither sudden nor catastrophic. The present complexity of the flora in that region is both a reflection and evidence of the long series of hybrid introgressions which have been taking place there. And it is the firm conviction of this reviewer that the

present baffling complexity of the flora of the Amazonian Basin can be laid to the geologically recent emergence of parts of the area after a possible brief marine invasion; therefore, the flora of much of the Amazonian lowlands would be of comparatively recent advent and so exhibit on a grand scale what one can see, in miniature, on a cut and burned-over woodland area into which a series of introgressive species had recently migrated. In brief, what one can observe after sudden catastrophies of nature open up new series of habitats, or where man disturbs an area, are only glimpses into what has been occurring on a much larger scale ever since the world was clothed with its first green mantle. It is not the sudden and perhaps spectacular catastrophe which is important; the important thing is that it leaves in its wake a series of new habitats into which organisms can venture, there to experiment with all possible combinations within their common pool of variant genes. The area of experimentation can be small or continental in extent.

From all sides one hears the lament of those who regret the necessity of studying populations under what they term "disturbed conditions." If it were possible they should ask that pool of genes which comprises the genus *Quercus* if it knows of such a thing as a really stable habitat. Were it able to answer it could tell of many events since the breaking dawn of the Cretaceous when, already, it was a large and lusty group: it could tell of great territories founded beneath the waves, of lands come up out of the sea, of mountain ranges that have reared their peaks into the zone of perpetual snow, of sharp crags worn down to softly contoured plains, of climatic changes in certain areas which ran the whole gamut of variability from subtropical to arctic or from rain-forest to desert, and of the waxing and waning of great groups of browsing or acorn-stealing animals. If the oak genes could talk they would say that there is no such thing as a stable habitat. Yet the oaks of today are no more and no less oaks than were their ancestors of the Cretaceous, and anyone who will bother to read the record in the rocks will see that, to keep the place they have in the world's flora in the face of widely differing and constantly changing habitats and conditions, it was often necessary to dip deeply into the common pool of basic genes with which the group was long ago endowed. The genic introgressions which we see so commonly in our modern oaks—to some a most startling and unusual series of phenomena—are probably no different either in their nature or magnitude from those which certainly must have taken place almost continually in the past. It is not the expected linear evolution of the oaks since the Cretaceous which primarily intrigues us; it is the reticulate nature of much of their post-Cretaceous evolution that astounds, a reticulum maintained throughout this long period solely by the phenomenon of introgressive hybridization.

For the taxonomist venturing for the first time from the conceptual confinement of herbarium study into an analysis of living populations in the green world outside, Dr. Anderson's little book will be a great comfort. From it he can learn much to assist him in understanding the basis and mechanics of the variability he is certain to encounter in some nearby stretch of woodland or a single meadow. From these introductory analyses he can proceed to adjacent areas; and so on, if need be, to encompass a whole continent with adequate sampling methods. First, however, let him be warned that his primary study of introgressive hybridization may be the opening of a veritable Pandora's box for, as he delves further within the secrets of the group he studies, he well may uncover such taxonomic ills as polyploidy, aneuploidy, apomixis, and other items which currently plague the workers in the new systematics. But if he be of stout heart and persistent, let him remember also that, underneath the ills, Hope lay at the bottom of Pandora's box—W. H. CAMP.

#### NOTE

The availability of money from the Mary S. Andrews Research Fund was announced in this journal, vol. 75, p. 585 and the grants appear in the Minutes of the meeting of April 5, 1949. The proposed uses are of wide interest. Dr. Robert Clausen of Cornell University, Ithaca, N. Y., has in mind "a taxonomic study of the genus *Sedum* in the

Sierra Madre Oriental of Mexico." Dr. Richard Goodwin, Connecticut College, New London, Conn., will continue "a study of fluorescing substances in roots." Dr. Goodwin reported to the Club on some of his studies of these substances at the meeting of April 5. Dr. Heimsch, University of Texas, Austin, Texas, wishes to make "comparative anatomical studies of angiospermous families." Brother Leon, Colegio de La Salle, Vedado, Habana, Cuba, will use his portion "to assist in the preparation of volumes on the 'Flora de Cuba.'"

In addition to the usual courses offered at the New York Botanical Garden this autumn there is to be one for beginners in the study of fungi. This will meet Saturday mornings, starting Sept. 17, for five weeks. Collecting and identification will be stressed with emphasis on distinguishing the poisonous from the edible forms.

# INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

## TAXONOMY, PHYLOGENY AND FLORISTICS

ALGAE, ETC.

(See also under Ecology. Williams)

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HISTORY OF AN ESTUARINE BOG AT SECAUCUS,  
NEW JERSEY<sup>1</sup>

C. J. HEUSSER

Large parts of the Hackensack tidal marsh in northeastern New Jersey were covered with extensive forests of southern white cedar (*Chamaecyparis thyoides*<sup>2</sup>) for some time in the recent past. These forests contained trees of such size as are unknown today along the coast of New Jersey. Large stumps and logs are evident over much of the area as illustrated in



FIG. 1. Logs and stumps revealed by ditching at Secaucus. Area once covered by cedar forest is now covered with the reed, *Phragmites communis*.

figure 1. At a number of places, the forests have been succeeded by marshes, and the stumps and logs have been completely buried in marsh

<sup>1</sup> This study was supported by grants from the research council of Rutgers University.

<sup>2</sup> The nomenclature of Gray's Manual, 7th Ed. (Robinson and Fernald, 1908) is followed throughout.



peat. Evidence of these forests can no longer be seen at the surface, but in some cases remains show up along ditches (fig. 2). Vermuele (1897), about the close of the last century, mapped this area and indicated the original outline of the cedar forests as well as the localities which at that time supported dense stands of living cedar.



FIG. 2. Ditching reveals remains of former cedar forest at Secaucus. Low tide aspect shows forest remains covered by marshland.

This paper represents a study of one of these former cedar bog forests and its associated marshlands at Secaucus, New Jersey. The problem was extended to include not only the disappearance of the white cedar forest and the subsequent invasion by the marsh, but also to trace the developmental history of the bog since the recession of the last of the Pleistocene ice. The investigations included a study of the present vegetation, the

underlying peat deposits, and the salinity of the tidal water. The Secaucus bog was chosen because of its position between two tidal creeks (fig. 3), namely Croma Kill and Mill Creek, and because its botanical history is so well known.

The Hackensack Valley in which the marsh is located occupies a portion of the Triassic plain of the piedmont of New Jersey. This valley is a broad lowland approximately 30 miles long, 5 miles wide at its southern end and about 2 miles wide at the north where it is crossed by the New

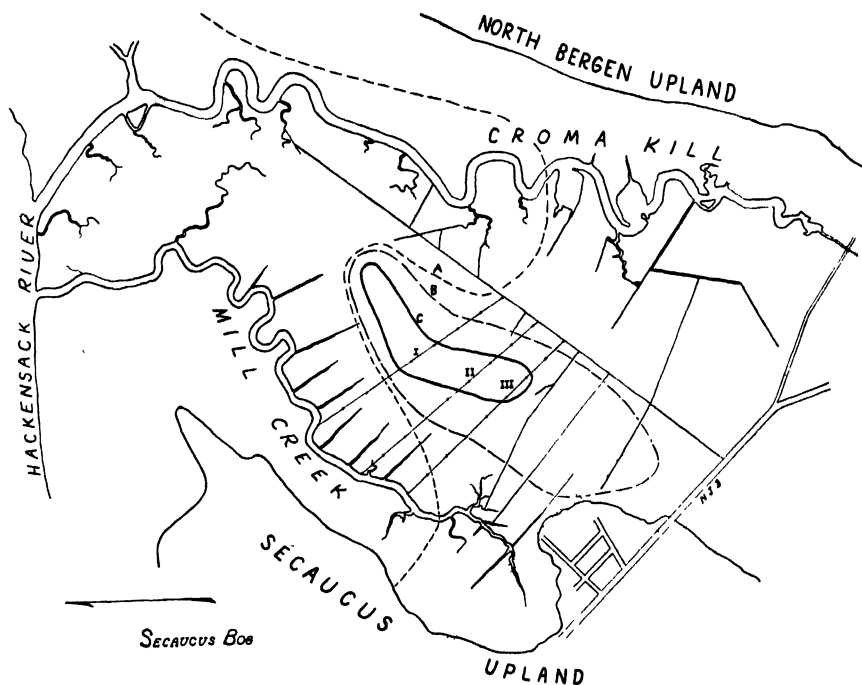


FIG. 3. Map of the Secaucus bog. Area between North Bergen upland and Secaucus upland is largely tidal marsh. South of the line made up of short dashes (A) to some extent beyond highway NJ-3 is the former area occupied by the cedar forest according to Vermeule (1897). The area within the long dash line (B) is covered with stumps and has been invaded by the marsh to line C. Line C represents the present extent of the bog. Lines I, II, and III refer to the respective north, middle, and south transects. Dots on these represent distances 100 meters apart. All other singly solid lines designate drainage ditches. New highway is shown in dotted lines.

York-New Jersey state line. On the east, the diabase sill of the Palisades forms a ridge, running parallel to the valley for its entire length. On the west, the Triassic shale and sandstone hills and the basaltic ridge known as the First Watchung form its western boundary. The lower end of the valley is today partly drowned by Newark Bay. Much more of it is occupied by an extensive area of tidal marsh and former cedar bogs extending to

about 10 miles north of Newark Bay. According to Vermuele (1897), at the beginning of this century, the marsh constituted an area of 20,045 acres, 1,465 acres of which were fresh meadow.

Since, as Waksman (1942) has pointed out, the terms swamp, bog, and marsh are loosely used, the following will clarify the usage as far as this paper is concerned. A swamp in the broad sense is a lowland community in which the ground is saturated with water for all or nearly all of the year. However, as considered here, more specifically, a swamp occupies an area in which the water table is at or very near the surface throughout the year, or at times the ground may be flooded. The underlying material is high in mineral matter. The vegetation consists of broad-leaved forest trees. A bog, on the other hand, is an area which has been built up by the accumulation of partially decayed organic material, and the vegetation consists largely of ericads, conifers, and mosses. A marsh, finally, is an area which is dominated by grasses, sedges, cattails, and rushes. While swamps and bogs are fresh water, a marsh may be fresh or saline and may or may not be underlain by an accumulation of organic remains.

**POST-PLEISTOCENE HISTORY.** The Wisconsin ice sheet covered the Hackensack Valley. It extended farthest south to a line connecting Morristown and Perth Amboy in New Jersey with Staten Island and Long Island in New York. With the retreat of the glacier, ice-front lakes developed as a result of the impounding of melt water either behind the moraine barrier or in northward draining valleys. In the Hackensack Valley, Lake Hackensack formed and was connected with Lake Hudson and Lake Flushing to the east (Reeds, 1933).

Sediments were carried into the basin of Lake Hackensack by water from the melting ice front and also from the surrounding region. These deposits consisted of clay, sand, gravel, and boulders. In much of the Hackensack Valley, laminated clay forms a considerable portion of the glacial drift. Reeds (1926, 1927) and Antevs (1922, 1928) have studied this varved clay at many places in the valley. Antevs (1928) concluded from his investigations that glacial Lake Hackensack existed for 2,500 to 3,000 years.

Although Salisbury (1902) considered Lake Hackensack connected with the sea in the form of a bay, Antevs (1922) contended that the area must have been a fresh water lake and not a bay of the sea. Antevs based this conclusion on the fact that the clays at Hackensack, New Jersey are distinctly varved. If the area had been covered by an arm of the sea shortly after the glacial lake formed, the clays would have been homogeneous for the most part, and only a few varves would have been distinguishable at the bottom. These bottom varves would then have comprised the only clay deposited under fresh water conditions. As a great number of varves were

deposited (more than 2,500 at Hackensack), Antevs (1922) further stated that the barrier damming the lake must have existed for a long time. The valley was depressed at the time the ice disappeared and was later uplifted. As the land was elevated (isostatic readjustment), the barrier damming the lake was obliterated. The terminal moraine may have acted as that barrier and if so would have been continuous during varve formation. If it were the barrier, there could have been no breaks where now Arthur Kill separates Perth Amboy from Staten Island and the Narrows separates Staten Island from Long Island.

According to Antevs (1928), while this region was depressed by the ice during the time Lake Hackensack was actively receiving drift sediments, the sea level was much lower than at present. His calculations show a lowering of sea level some 300 feet at the climax of the glacial period. Land which is now submerged constituted a wide coastal plain, which in New Jersey probably extended some 80 miles beyond the present sea shore. Of course the sea level must have come up during the existence of glacial Lake Hackensack due to melt water returning to the oceans. This rise of the sea was probably slow, so that a long time elapsed before the sea was level with the southern end of the Lake Hackensack basin. The present study would indicate that Lake Hackensack had drained by that time.

RECENT BOTANICAL HISTORY. During the nineteenth century, this area at Secaucus was known to botanists as the New Durham cedar swamp. When John Torrey wrote his "Catalogue of Plants Growing Spontaneously Within Thirty Miles of the City of New York" in 1819, he made special reference to the bog. The plants Torrey collected in the bog are included in this catalogue, labelled specifically "from the cedar swamp, New Durham." These plants are a valuable record inasmuch as they represent the natural flora of the bog during a rather early period. Such plants as *Calla palustris*, *Coptis trifolia*, *Cornus canadensis*, *Chiogenes hispidula*, and *Vaccinium oxycoccus* were found. Many of the plants possess a distinctly boreal affinity. Such plants as *Picea mariana* and *Larix laricina* reached their known south-easterly limit here.

Following Torrey's work, a period of over half a century elapsed before any further record of the flora of the bog is known to have been published. In 1881, Britton listed a number of plants which are not found in Torrey's catalogue. Shortly after, Britton published his "Catalogue of Plants Found in New Jersey" (Britton, 1889). In this work, a number of newly found plants were recorded. Many of the plants catalogued by Torrey persisted to this date. Especially to be noted in Britton's 1889 flora is the occurrence of *Picea mariana* and *Larix laricina*.

In 1919, Harshberger and Burns presented a study of the vegetation of

the Hackensack marsh, but no mention of growing white cedar is included. They appear not to have visited the Secaucus bog. By 1919, the cedar forests were probably largely destroyed. However, in April of 1949 about half a dozen trees of white cedar were found growing in a bog at Moonachie on the other side of the Hackensack River from Secaucus. In conversation with Mr. James L. Edwards of Montclair, New Jersey, the author learned that the last trees of white cedar in the Secaucus bog died about 1935.

In 1943, Waksman and co-workers investigated the peat underlying the bog. This is the most recent of the studies made in the area. It was not concerned with the individual kinds of plants present. The authors mapped the bog and the surrounding marsh and gave a rough description of the vegetation. They also constructed a peat profile showing the distribution of the kinds of peat.

#### METHODS

**VEGETATION.** For sampling the present vegetation of the Secaucus bog, the transect method was used. Three transects were laid out from Mill Creek on the northwest side of the bog to a wide drainage ditch on the southeast side (see map, figure 3). The transect lines were placed in such a way as not to cross the drainage ditches running into Mill Creek. In general, they were between 100 and 200 meters apart and from north to south were respectively named the "north," "middle," and "south" lines. This terminology is followed throughout the paper.

The middle transect was the longest. It ran approximately south  $25^{\circ}$  east from the bank of Mill Creek for a distance of 825 meters. The north line ran south  $22^{\circ}$  east for 803 meters, and the south line ran south  $30^{\circ}$  east for 795 meters. All lines were laid out with tape and compass, and stakes were placed 20 meters apart beginning with the initial stake at the bank of Mill Creek.

The object of the vegetational analysis was to obtain cover data. Cover was determined by the use of the numerical evaluation system of Braun-Blanquet (1932). For every 10 meter segment on all three transects, the cover of each species was estimated for the aestival and autumnal aspects. This was done at both seasons with tape and string using the 20 meter stakes as a guide.

**SALINITY.** For the determination of the salinity of the surface water, the method outlined by Denny (1927) was employed. Water samples were collected at every 20 meters on each transect during one period of incoming tide for the spring, summer, and fall. A further salinity study for comparative purposes was conducted approximately 30 miles south of Secaucus at Cheesequake marsh on Raritan Bay. This area was chosen because of the presence of a forest of living white cedar which grades into a brackish

marsh. On a transect running for a distance of 30 meters from within the forest out onto the marsh, water samples were taken at one meter intervals during one period of incoming tide in the summer and fall. All samples obtained in the field at Secaucus and at Cheesequake were brought back to the laboratory. Cover data for the white cedar and other forest plants as well as the marsh species were obtained along this transect.

The water samples collected at Cheesequake and Secaucus were taken on incoming tides on about the same date in the summer and fall, but the height of the tides was different at the two places for the different times of sampling. Sampling was done at Secaucus for the summer and fall on 21 July and 26 September 1948, respectively. From the "Tide Tables Atlantic Ocean for the Year 1948" (1947), the maximum height of the tide at Secaucus was found to have been about 4.9 feet and 4.4 feet for these respective dates. These figures are compared to maximum tidal heights of approximately 5.0 feet and 5.6 feet for 24 July and 24 September at Cheesequake marsh.

On the basis of the above information, there was a difference of only 0.1 foot between the maximum tidal heights at Secaucus and at Cheesequake for July. This little difference would thus allow salinity determinations comparable between these two places. However, the difference in the maximum tidal heights for September was 1.2 feet which precludes any comparison between the two places at that time.

**PEAT.** The peat was sampled by means of the Davis type American peat sampler. Stations were established 100 meters apart on all transects beginning with the initial stations at the bank of Mill Creek (dots on transect lines, fig. 3). Samples were obtained at one foot intervals at each 100 meter station to an approximate depth of 10 feet at which level gray clay was usually encountered. In all cases, sampling was done until the basement clay was reached. The peat from each level was examined in the field, and representative portions were brought back to the laboratory.

The purpose of the study was to construct profiles of the underlying peat along each transect. Field notes were used as the basis for these profiles. In the construction of the profile for the middle transect, laboratory data were used in addition to field notes. The peat from each level from stations 0, 100, 200, and 300 meters on the middle transect was examined in the laboratory under a binocular microscope at 15 $\times$ . Fragments of the plant material, roots and rhizomes of herbaceous plants, small bits of wood, and fruits, were processed for identification by Benninghoff's (1947) technique. Identification of the wood was made through the use of the keys of Brown, Panshin, and Forsaith (1949) and Record (1934). In addition, slides of known species were compared. The herbaceous peat was identified by comparison with prepared slides of known species.

## RESULTS

**VEGETATION.** The total number of species present in the bog and the surrounding marsh is 117. These are listed in table I. The cover for representative species on the middle transect is presented in figure 4. These data are essentially similar to those obtained from the north and south transects. They show the degree of dominance of the species and their distribution in space at two different seasons. For example, *Phragmites communis* and *Typha angustifolia* have both a broad distribution and a high degree of

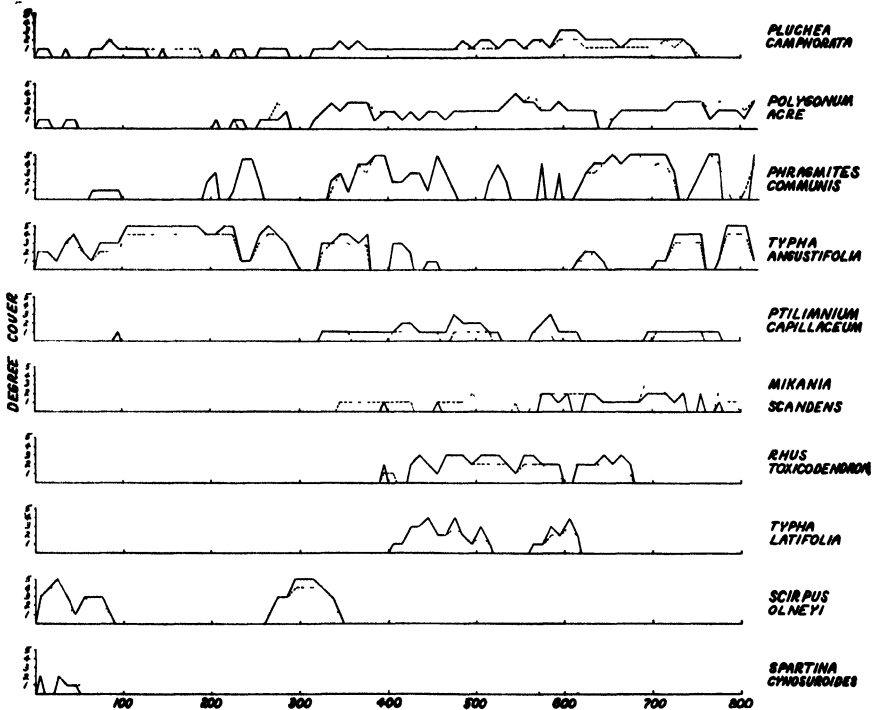


FIG. 4. Distribution and dominance of a few of the important species represented on the middle transect at Secaucus. Solid lines indicate results of summer sampling while the dotted lines those of fall sampling. Where only solid lines appear, there is indicated no change in the dominance and distribution of the species.

cover. *Scirpus olneyi*, on the other hand, has a high cover value where it occurs, but its distribution is more limited. Other plants such as *Typha latifolia* and *Rhus toxicodendron* occur only in the bog, while *Pluchea camphorata* and *Polygonum acre* are distributed for almost the entire length of the middle transect. These latter species have the widest distribution of all, occurring on approximately three-fourths of all the segments sampled. Also apparent is the great extent of *Phragmites communis* and *Typha angustifolia* (fig. 4).

TABLE I. *Plant list for the Secaucus bog and surrounding marshland for 1948. The order of plants follows that of Gray's Manual, 7th Ed. (Robinson and Fernald, 1908).*


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<i>Aspidium thelypteris</i>	<i>Rubus</i> sp.
<i>Onoclea sensibilis</i>	<i>Apios tuberosa</i>
<i>Osmunda cinnamomea</i>	<i>Rhus copallina</i>
<i>Osmunda regalis</i>	<i>Rhus toxicodendron</i>
<i>Typha angustifolia</i>	<i>Ilex verticillata</i>
<i>Typha latifolia</i>	<i>Acer rubrum</i>
<i>Alisma plantago-aquatica</i>	<i>Impatiens biflora</i>
<i>Sagittaria latifolia</i>	<i>Rhamnus frangula</i>
<i>Agrostis hyemalis</i>	<i>Psedera quinquefolia</i>
<i>Cinna arundinacea</i>	<i>Vitis labrusca</i>
<i>Distichlis spicata</i>	<i>Hibiscus moscheutos</i>
<i>Echinochloa walteri</i>	<i>Hibiscus oculiroseus</i>
<i>Glyceria nervata</i>	<i>Hypericum virginicum</i>
<i>Panicum virgatum</i>	<i>Viola pallens</i>
<i>Phragmites communis</i>	<i>Lythrum salicaria</i>
<i>Spartina cynosuroides</i>	<i>Cicuta maculata</i>
<i>Spartina glabra</i> var. <i>pilosa</i>	<i>Ptilimnium capillaceum</i>
<i>Spartina michauxiana</i>	<i>Sium cicutaefolium</i>
<i>Spartina patens</i>	<i>Nyssa sylvatica</i>
<i>Zizania aquatica</i>	<i>Clethra alnifolia</i>
<i>Cyperus nuttallii</i>	<i>Gaylussacia frondosa</i>
<i>Cyperus strigosus</i>	<i>Leucothoe racemosa</i>
<i>Eleocharis palustris</i>	<i>Rhododendron viscosum</i>
<i>Scirpus americanus</i>	<i>Vaccinium atrocoecum</i>
<i>Scirpus olneyi</i>	<i>Vaccinium corymbosum</i>
<i>Scirpus robustus</i>	<i>Vaccinium corymbosum</i> var. <i>amoenum</i>
<i>Scirpus validus</i>	<i>Lysimachia thyrsiflora</i>
<i>Peltandra virginica</i>	<i>Asclepias incarnata</i> var. <i>pulchra</i>
<i>Lemna minor</i>	<i>Convolvulus sepium</i>
<i>Juncus gerardi</i>	<i>Cuscuta compacta</i>
<i>Hemerocallis fulva</i>	<i>Verbena hastata</i>
<i>Maianthemum canadense</i>	<i>Lycopus uniflora</i>
<i>Smilax rotundifolia</i>	<i>Scutellaria galericulata</i>
<i>Iris versicolor</i>	<i>Solanum dulcamara</i>
<i>Betula populifolia</i>	<i>Sambucus canadensis</i>
<i>Quercus bicolor</i>	<i>Viburnum dentatum</i>
<i>Quercus palustris</i>	<i>Viburnum nudum</i>
<i>Quercus rubra</i>	<i>Viburnum prunifolium</i>
<i>Boehmeria cylindrica</i>	<i>Ambrosia artemisiifolia</i>
<i>Pilea pumila</i>	<i>Aster novi-belgii</i>
<i>Polygonum acre</i>	<i>Aster subulatus</i>
<i>Polygonum arifolium</i>	<i>Baccharis halimifolia</i>
<i>Polygonum hydropiperoides</i>	<i>Bidens connata</i>
<i>Polygonum mühlenbergii</i>	<i>Bidens laevis</i>
<i>Polygonum sagittatum</i>	<i>Bidens trichosperma</i>
<i>Polygonum scandens</i>	<i>Erechtites hieracifolia</i>
<i>Rumex britannica</i>	<i>Eupatorium perfoliatum</i>
<i>Atriplex patula</i>	<i>Eupatorium purpureum</i>
<i>Acnida cannabina</i>	<i>Gnaphalium polycepalum</i>
<i>Phytolacca decandra</i>	<i>Helianthus giganteus</i>
<i>Caltha palustris</i>	<i>Mikania scandens</i>
<i>Ranunculus sceleratus</i>	<i>Pluchea camphorata</i>
<i>Thalictrum polygamum</i>	<i>Solidago elliotii</i>
<i>Radicula nasturtium-aquaticum</i>	<i>Solidago graminifolia</i>
<i>Radicula palustris</i> var. <i>hispida</i>	<i>Solidago rugosa</i>
<i>Amelanchier oblongifolia</i>	<i>Solidago scabra</i>
<i>Pyrus arbutifolia</i> var. <i>atropurpurea</i>	<i>Solidago sempervirens</i>
<i>Prunus serotina</i>	<i>Solidago serotina</i>
<i>Rosa carolina</i>	

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Seasonal aspect is important in the study of the bog and marsh vegetation. *Ptilimnium capillaceum* and *Mikania scandens*, although well distributed, vary as to the time they reach their maximum cover, *Ptilimnium* reaching its peak of development during the summer, *Mikania* in the early autumn. It was because of this change of seasonal aspect that the two periods of study were undertaken. The members of the Compositae, for further example, were apparent during the summer, but it was during the fall sampling that they became important. Of interest with regard to *Mikania* is its frequent ability to spread over large areas of *Phragmites*, bending them down to about waist height.



FIG. 5. Central portion of the Secaucus bog showing the remains of the former cedar forest.

Zonation is apparent in the distribution of plants surrounding the central portion of the former cedar bog. Figure 4 shows this in both the dominance and distribution of the plants. The species of *Spartina* are found along Mill Creek. *S. cynosuroides* occurs as far back from the bank as 70 meters (average about 30 meters), while *S. michauxiana* extends to about 20 meters, and *S. glabra* var. *pilosa* is found only on the immediate bank. This group along with sparse patches of *Juncus gerardi* occupy the area of greatest salt concentration. Behind this, *Typha angustifolia* and *Scirpus olneyi* make up a zone approximately 250 meters broad. These species vary in dominance, often occurring mixed or separate, with *Typha* having a

greater cover and more continuous distribution than *Scirpus*. Near the *Spartina* zone, *Scirpus olneyi* is often mixed with small amounts of *Scirpus americanus*. Back from the *Typha-Scirpus* zone, *Scirpus olneyi* forms an almost pure belt about 30 meters wide which then gives way to a preponderance of *Phragmites communis*. The *Phragmites* zone immediately surrounds the central area of the bog. In many places in the bog, *Phragmites* now forms small colonies. These have undoubtedly developed since the disappearance of the forest. *Phragmites* also occurs in colonies throughout the marsh.

Figure 5 shows the condition of the remains of the former white cedar forest. This remnant of the former, more extensive forest today measures roughly 1000 by 150 meters and is a dense entanglement of shrubs and small trees, both living and dead. The living vegetation is partly made up of the woody plants *Rhododendron viscosum*, *Clethra alnifolia*, *Vaccinium* spp., *Amelanchier oblongifolia*, *Rhamnus frangula*, and *Ilex verticillata*. Both dead and young living trees of *Nyssa sylvatica*, *Quercus bicolor*, *Acer rubrum*, and *Betula populifolia* are scattered among the shrubs. The predominant herb species are *Pluchea camphorata*, *Polygonum acre*, and *Ptilimnium capillaceum*.

The results of the study at Cheesequake marsh reveal the cedar forest to be made up of *Chamaecyparis thyoides* with *Acer rubrum* of secondary importance. Along the transect, the cedars were all found to be small trees. They grade for the most part from individuals only slightly greater than 1 inch d.b.h. (diameter breast high) to small saplings where the edge of the forest makes contact with the marsh. The largest trees on the transect are 5 inches d.b.h. Seedlings of white cedar are fairly well dispersed throughout the forest and are scattered beyond the margin of the forest on the marsh. A few small saplings are growing beyond the limit of the occurrence of seedlings.

In the cedar forest, *Vaccinium corymbosum*, *Ilex verticillata*, *Rhododendron viscosum*, *Clethra alnifolia*, and *Magnolia virginiana* are scattered throughout. As the forest becomes lower in stature on meeting with the marsh, the canopy opens and such plants as *Osmunda regalis*, *Vaccinium macrocarpon*, *Sanguisorba canadensis*, *Rhus toxicodendron*, and *Cladium mariscoides* are found along with the white cedar and red maple. On the adjacent part of the marsh, the vegetation consists predominantly of *Cladium mariscoides* with lesser amounts of *Panicum virgatum*. Although the marsh continues for 150 meters beyond the transect before Cheesequake Creek is reached, the study was terminated at 30 meters due to the presence of an artificial drainage ditch. The greater part of the marsh beyond the ditch consists of *Spartina patens*, *Distichlis spicata*, *Eleocharis rostellata*, and *Scirpus americanus*.

**SALINITY.** The results of the salinity determinations for the middle transect at Secaucus, expressed in both per cent of sea water and parts per thousand of chlorides, are given in figure 6. The curves for the salinities on the three transects for spring, summer, and fall show a similar trend. On all the curves there is a distinct increase in salinity for the summer and fall over that of the spring. For example, the salinities in the marsh for the spring determination at 300 meters from Mill Creek on the north, middle, and south lines respectively were 5.80, 4.80, and 6.10 per cent sea water. At the same stations in the summer, they were 8.60, 7.35, and 8.40 per cent; and for the fall, the results were 23.50, 20.35, and 20.10 per cent. The salinities for the spring at points within the bog 500 meters from Mill Creek likewise on the north, middle, and south lines respectively were 4.30, 4.55,

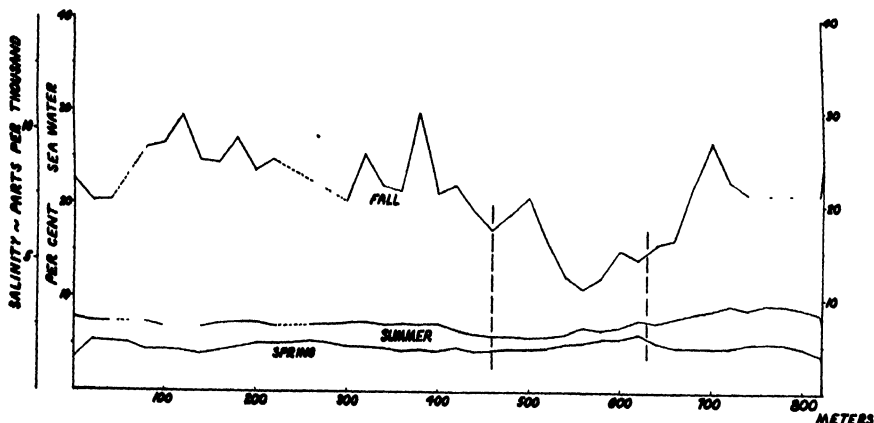


FIG. 6. Salinity curves for the middle transect at Secaucus for the spring, summer, and fall sampling. Irregularities in the fall curve are due to high evaporation and extremely low rainfall following a neap tide. Dotted lines indicate no sample determination at the particular station. Upright dash lines set off the open portion of the bog.

and 5.10 per cent sea water. At the same stations for the summer, they were 5.80, 5.80, and 6.95 per cent and for the fall 14.15, 20.75, and 14.90 per cent. The curves for the spring and summer on all the transects are rather smooth and show no pronounced irregularity while those for the fall show marked irregularity. Especially significant, as illustrated in figure 6, are the lower salinities in the open bog (area between broken lines in figure 6) and the area immediately on either side. Although these lower salinities are not striking on the spring and summer curves, the fall curves show this very well in the low dip that occurs as the bog is reached.

Although spring salinities were not determined at Cheesequake marsh, the results of the summer and fall sampling show an increase in fall salinity over that of summer similar to that found at Secaucus. At a point on the

marsh 6 meters out from the last cedar sapling, the salinity reached 7.55 per cent sea water in July. This was the highest salinity on the transect at that time. In September, the salinity at this same point reached 34.20 per cent sea water which was nearly the highest recorded at that date. The maximum salinity in the vicinity of the growing cedar was 2.60 per cent during the time of the summer study. During the fall the maximum had greatly increased to 28.10 per cent.

A comparison between the minimum salinities recorded during the summer in the former cedar bog at Secaucus and the maximum salinity determined in the vicinity of the living cedar at Cheesequake at the same time, reveals a higher salinity at Secaucus. While in the Secaucus bog on the north, middle, and south transects respectively, minimum salinities in July were recorded at 5.10, 5.80, and 6.90 per cent sea water, at Cheesequake the maximum salinity for the living cedar at that time was 2.60 per cent. This maximum salinity of 2.60 per cent is even lower than the minima recorded in the cedar bog at Secaucus for the spring: 3.90, 4.40, and 4.90 per cent on the respective north, middle, and south lines. The salinity at Cheesequake during the spring, although not studied, was probably less than 2.60 per cent.

It is interesting to note that during the time of the fall determinations, the minimum salinities in the Secaucus bog were below rather than above the maximum salinity beneath the growing cedar at Cheesequake. At Secaucus, the minimum salinities recorded during the fall on the north, middle, and south lines respectively were 12.30, 11.00, and 12.35 per cent sea water. At Cheesequake in the vicinity of the living cedar, the maximum salinity at any time was 28.10 per cent. In other words, cedar is growing at Cheesequake where occasionally it is subjected to tidal water which is highly saline. In the above case, the water was even more highly saline than in the Secaucus bog where the cedar is no longer growing. As mentioned earlier, however, it was a higher tide at Cheesequake than at Secaucus at the time the fall determinations were made.

Precipitation data kindly furnished by the U. S. Department of Commerce Weather Bureau at Newark, New Jersey (about six miles southwest of Secaucus and about twenty-five miles northwest of Cheesequake) show that monthly precipitation totals were approximately similar during June and July (the time at which the spring and summer sampling was done) with 6.19 and 6.88 inches, respectively. In September, at which time the salinities had greatly increased, the precipitation for the month reached a low for the year at 1.14 inches. This information is significant in showing the relationship between the precipitation and the salinity data.

PEAT. The peat in the profile for the middle transect consists for the

**SALINITY.** The results of the salinity determinations for the middle transect at Secaucus, expressed in both per cent of sea water and parts per thousand of chlorides, are given in figure 6. The curves for the salinities on the three transects for spring, summer, and fall show a similar trend. On all the curves there is a distinct increase in salinity for the summer and fall over that of the spring. For example, the salinities in the marsh for the spring determination at 300 meters from Mill Creek on the north, middle, and south lines respectively were 5.80, 4.80, and 6.10 per cent sea water. At the same stations in the summer, they were 8.60, 7.35, and 8.40 per cent; and for the fall, the results were 23.50, 20.35, and 20.10 per cent. The salinities for the spring at points within the bog 500 meters from Mill Creek likewise on the north, middle, and south lines respectively were 4.30, 4.55,

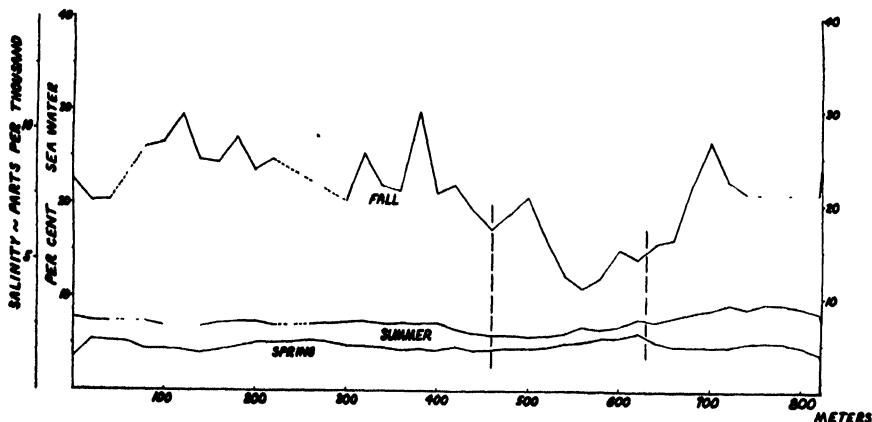


FIG. 6. Salinity curves for the middle transect at Secaucus for the spring, summer, and fall sampling. Irregularities in the fall curve are due to high evaporation and extremely low rainfall following a neap tide. Dotted lines indicate no sample determination at the particular station. Upright dash lines set off the open portion of the bog.

and 5.10 per cent sea water. At the same stations for the summer, they were 5.80, 5.80, and 6.95 per cent and for the fall 14.15, 20.75, and 14.90 per cent. The curves for the spring and summer on all the transects are rather smooth and show no pronounced irregularity while those for the fall show marked irregularity. Especially significant, as illustrated in figure 6, are the lower salinities in the open bog (area between broken lines in figure 6) and the area immediately on either side. Although these lower salinities are not striking on the spring and summer curves, the fall curves show this very well in the low dip that occurs as the bog is reached.

Although spring salinities were not determined at Cheesequake marsh, the results of the summer and fall sampling show an increase in fall salinity over that of summer similar to that found at Secaucus. At a point on the

marsh 6 meters out from the last cedar sapling, the salinity reached 7.55 per cent sea water in July. This was the highest salinity on the transect at that time. In September, the salinity at this same point reached 34.20 per cent sea water which was nearly the highest recorded at that date. The maximum salinity in the vicinity of the growing cedar was 2.60 per cent during the time of the summer study. During the fall the maximum had greatly increased to 28.10 per cent.

A comparison between the minimum salinities recorded during the summer in the former cedar bog at Secaucus and the maximum salinity determined in the vicinity of the living cedar at Cheesequake at the same time, reveals a higher salinity at Secaucus. While in the Secaucus bog on the north, middle, and south transects respectively, minimum salinities in July were recorded at 5.10, 5.80, and 6.90 per cent sea water, at Cheesequake the maximum salinity for the living cedar at that time was 2.60 per cent. This maximum salinity of 2.60 per cent is even lower than the minima recorded in the cedar bog at Secaucus for the spring: 3.90, 4.40, and 4.90 per cent on the respective north, middle, and south lines. The salinity at Cheesequake during the spring, although not studied, was probably less than 2.60 per cent.

It is interesting to note that during the time of the fall determinations, the minimum salinities in the Secaucus bog were below rather than above the maximum salinity beneath the growing cedar at Cheesequake. At Secaucus, the minimum salinities recorded during the fall on the north, middle, and south lines respectively were 12.30, 11.00, and 12.35 per cent sea water. At Cheesequake in the vicinity of the living cedar, the maximum salinity at any time was 28.10 per cent. In other words, cedar is growing at Cheesequake where occasionally it is subjected to tidal water which is highly saline. In the above case, the water was even more highly saline than in the Secaucus bog where the cedar is no longer growing. As mentioned earlier, however, it was a higher tide at Cheesequake than at Secaucus at the time the fall determinations were made.

Precipitation data kindly furnished by the U. S. Department of Commerce Weather Bureau at Newark, New Jersey (about six miles southwest of Secaucus and about twenty-five miles northwest of Cheesequake) show that monthly precipitation totals were approximately similar during June and July (the time at which the spring and summer sampling was done) with 6.19 and 6.88 inches, respectively. In September, at which time the salinities had greatly increased, the precipitation for the month reached a low for the year at 1.14 inches. This information is significant in showing the relationship between the precipitation and the salinity data.

PEAT. The peat in the profile for the middle transect consists for the

most part of two main types: marsh peat and forest peat (fig. 7). Marsh peat forms a layer for approximately 300 meters in from Mill Creek, overlying forest peat. It is deep at the creek and thins out gradually becoming merely a superficial layer as the bog is approached. Marsh peat also overlies forest peat on the east side of the bog.

The marsh peat is almost everywhere a black, well-consolidated, highly organic material, made up largely of *Scirpus olneyi* mixed at some levels with *Juncus gerardi* and at others with *Typha angustifolia*. At Mill Creek, there is a deposit of silt extending to a depth of 8 feet. This silt occurs as a superficial layer over much of the marsh back from the creek (specifically the area above the broken and dotted line in figure 7). Some reed peat made

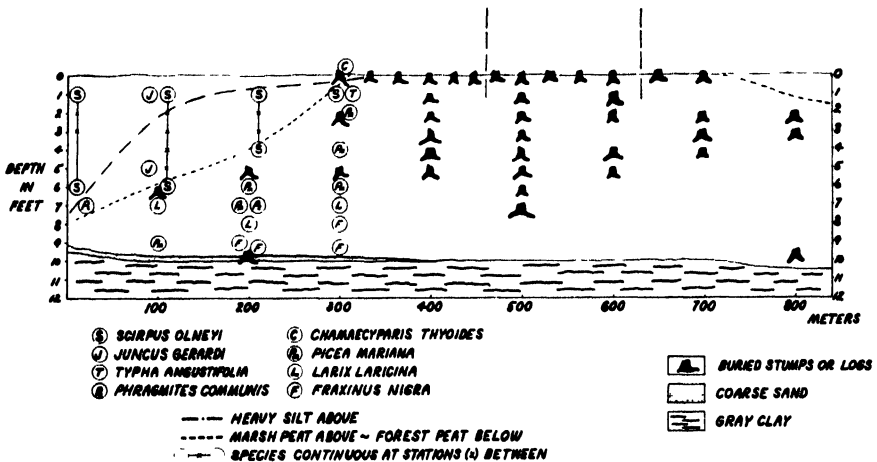


FIG. 7. Peat profile for the middle transect at Secaucus. Although not shown, angiospermous peat occurs at the bottom at stations 0 and 100 as well as 200 and 300 meters. Upright dash lines set off the open portion of the bog.

up of rhizomes of *Phragmites communis* is found at 7 feet at stations 0 and 200 meters.

Forest peat forms the bulk of the underlying plant remains for the middle transect (fig. 7). Within the area of the present bog and to some extent on either side, this type of peat is continuous from the bottom of the profile to the top. However, beyond this, it becomes overlain by an increasing depth of marsh peat. By and large, the forest peat is soupy, poorly consolidated, and colored a reddish-brown which is generally characteristic of coniferous peat.

Peat was analyzed at stations 0, 100, 200, and 300 meters on the middle transect. At station 300 meters which is the only station of the four analyzed where woody remains extend from bottom to top, there is an apparent gradation and layering of species in the vertical profile. The bottom layer

directly above the sand and clay consists for the most part of angiospermous woody plants with *Fraxinus nigra* especially evident. This layer is about 2½ feet in thickness with a darker color and is well-consolidated in contrast to the upper layers. From the 7 foot level to about 2 feet, *Picea mariana* and *Larix laricina* appear to be mixed. Stumps of *Chamaecyparis thyoides* are found at the surface. Marsh peat has accumulated about 6 inches deep about the bases of these stumps, so that they are partly buried.

The angiospermous peat layer is continuous over the bottom at the four stations studied. The *Picea-Larix* layer thins out as Mill Creek is approached and finally ends at station 100 meters. *Picea* and *Larix* were difficult to identify. At stations 200 and 300 meters, at 8 and 7 feet, respectively, cones of *Larix* and spur shoots characteristic of *Larix* were observed in the peat. The identification of the wood found at these levels as *Larix* was thus strengthened by this evidence.

Throughout the woody peat, regardless of the consolidation of the material, stumps and logs are buried at nearly all depths. At some stations, especially those within the bog itself, sampling was difficult due to the extensive occurrence of buried tree trunks. Although the profiles of the north and south transects are not presented, they illustrate the stratification of stumps and logs and also the overriding of the marsh peat upon the forest peat.

The basement material beneath the bog is gray consolidated clay. Variable amounts of sand are found above the clay, especially near Mill Creek. From information kindly given by the New Jersey State Highway Department for a sampling station near the fork in route N J-3 east of Secaucus (fig. 3), it was learned that the underlying material consists of gray clay to a depth of about 18 feet, soft brown clay to a depth of approximately 57 feet, and soft reddish clay with some pebbles to 102 feet. At this level sampling was discontinued.

The road building operations of the N. J. State Highway Department through the southern end of the former cedar bog are of interest in regard to the peat deposit (road in dotted lines in figure 3). The author has called attention to the large logs and stumps which were removed during these operations (Heusser, 1949).

#### DISCUSSION

The developmental history of the Secaucus bog has been greatly influenced by glacial activity and especially by the post-Wisconsin rise in sea level. In the peat underlying the bog, the remains of forests which formerly covered the area are evident. These forests became preserved as a result of the rise of the sea. In the Secaucus bog, this is clearly recorded in the gradual spread of the marsh deposits at the expense of the forest peat.

Long before glacial Lake Hackensack drained, the sea level had been



rising as a consequence of the increase of melt water returning to the oceans. This rise has been irregular throughout, caused by minor fluctuations in the ice during deglaciation and isostatic readjustment (Flint, 1947; Marmner, 1948). Some time during the period that the sea was coming up, the bed of glacial Lake Hackensack was uplifted, tilted and the lake drained. The clay and sand, deposited in the lake basin as the glacier retreated, were thereby exposed. The lake bed was thus free to receive the initial waves of invading plants. As the exposed basin was flat and probably poorly drained, only those species capable of growing under such conditions migrated into the area.

In the vicinity of Secaucus, it appears that *Fraxinus nigra* was among the first major forest species to have left a record. This is shown in the peat profile for the middle transect. It is unknown whether or not any forests preceded this black ash swamp. Conifer forests consisting possibly of fir may have existed prior to the ash, but no record of such forests was evident at Secaucus. The forest record only began when conditions became favorable for peat formation.

It is unknown how long the black ash swamp existed at Secaucus. After it was invaded by *Picea mariana* and *Larix laricina*, *Fraxinus nigra* persisted for a time mixed with larch and black spruce, but was ultimately succeeded by the latter two species which were favored by the rising water table. It is of interest to note that at Budd Lake, New Jersey, about 40 miles west of Secaucus, the converse of the above succession is occurring where black ash is slowly growing out on to a mat occupied by larch and black spruce, as the per cent of minerals in the peat increases. The above is a typical upland northern bog succession, but this situation reverses in an estuarine bog on a submerging coast as at Secaucus.

In interpreting this succession from a hardwood forest to one of larch and spruce, the change in the level of the water table must be taken into consideration. As the sea entered the southern end of the basin, the water table was raised. With continued encroachment of the land by the sea, the water table continued to rise higher and higher. Bartlett (1909) has called attention to this condition in his study of the *Chamaecyparis* bog at Woods Hole, Massachusetts. Black ash could not persist when the water table became critically high and raw peat began to accumulate rapidly. With the increase in the height of the water table, rapid peat formation was made possible and black spruce and larch with their associated vegetation invaded.

The dominance of *Picea* and *Larix* continued for a long time. With the persistent rise of the water table as the sea level came up, the bog grew upward. Only those species capable of living under such conditions could remain. Larch and black spruce were able to withstand the perpetuation of

these conditions. Their persistence up to the end of the nineteenth century is evidence of this.

Evidence of the continued increase of sea level is found in (1) the superposition of stumps and logs in the profiles, (2) the phenomenon of marsh peat overriding forest peat, and (3) the amount of silt carried over the marsh bordering the bog. The trees as they died were buried by the peat as the sea level came up. Marsh peat has impinged upon the forest as a consequence of increased tidal flooding from Mill Creek on the west and Croma Kill on the east. As the tides penetrated further into the bog, silt deposition in the peat was likewise coincident with the extent of the tidal flooding.

The entrance of brackish water into the area on the west side of the bog is not entirely evident until some time after the development of the spruce-larch forest. At station 0 meters on the middle transect at the bank of Mill Creek (fig. 10), the brackish water indicator plant, *Scirpus olneyi*, first appears in the profile at the 6 foot level. At 4 and 5 feet above, occurs a deposit of silt which does not contain plant remains. This is indicative of a certain amount of shifting in the channel bed in the course of centuries.

Since the first presence of brackish water in the Secaucus area, the rise of the sea level, as indicated by the marsh peat in the profile for the middle transect, has been essentially continuous. The effect of the sea rise is best shown on the west side of the bog where the gradient of marsh peat overlying forest peat is steeper than on the east. This is due to the fact that the bog is nearer Mill Creek than Croma Kill (see fig. 3), and the tides are consequently more effective from Mill Creek.

In the profile for the middle transect, *Chamaecyparis thyoides* is found only at or near the surface. As no remains of white cedar are evident except at or near the surface, one is led to conclude that this species migrated into the Secaucus bog rather recently after a long period of spruce-larch dominance. According to Torrey (1819), at the beginning of the nineteenth century: "The cedar swamp . . . is entirely overgrown with the *Cupressus thyoides* or white cedar, and other evergreens." The coniferous forest at that time appears to have consisted largely of cedar in which larch and black spruce were less abundant. White cedar, possessing a more austral affinity, presumably migrated up the coastal plain from a southern distribution center, following a long time after the spruce-larch immigration.

The profile Waksman and his co-workers (1943) present for the bog is based upon a generalized classification of the types of peat rather than specific plant remains. They show buried "stumps" and forest peat and overlying marsh peat. What is labelled "*Carex*" peat type is presumed to be *Scirpus* peat. The portion of the profile designated as "water" was not found by the author. Possibly they refer to soupy peat which, however, was

found underlying practically the entire bog portion and even parts of the surrounding marsh. Also, the material designated as "clay" and shown below the bog and up to the surface on the borders is not the same material throughout. Rather, what underlies the bog is consolidated gray clay of glacial origin. The material shown bordering the bog is heavy silt brought in during the rise of sea level.

Since early times when the first settlers occupied the Hackensack area, the cedar forests were exploited for such purposes as ship building and road building. Van Winkle (1924) tells of the early laying of corduroy roads from split cedar logs. One such road was built by John Schuyler as early as 1759. Van Winkle also mentions the cedar forests as a source of Christmas greens which were no doubt cedar and spruce.

This exploitation must have damaged these forests, but the destruction done by fire, mosquito ditching, and dyking was far more effective. As far back as the beginning of the eighteenth century, fire is known to have ravaged the Hackensack area (Van Winkle, 1924). In fact at that particular time, the area was purposely burned to force pirates and robbers from hiding in the cedar forests. Since then, the frequency of fire has gradually increased, so that today fire is a very common occurrence in the region especially in the fall and early spring.

Much of the area was formerly cut for "salt grass" (*Spartina patens* and *Distichlis spicata*) and "three square" (*Scirpus olneyi*). This cutting seemed, incidentally, to prevent fire, as the stubble that was left was not much of a fire hazard. The salt grass was used a great deal as bedding for horses, but with the advent of the automobile, the horse disappeared and likewise, the cutting on the marsh gradually stopped. Fires which then started, burned through extensive areas without being checked. Largely as a consequence of the increase of fire, the cedar forests were eventually destroyed.

Ditching has been exceedingly important in changing the drainage pattern and thus greatly effecting this distribution of salt and fresh water. Vermeule (1897) showed the distribution of artificial drainage ditches already constructed in 1896. Bog areas beyond the tide fed by run-off from the upland, springs, and by rainfall were thereby more rapidly drained while outer margins received greater influence of tidal flooding. The cedar forests were thus affected in the course of the ditching due to a greater influx of saline water. In some cases, dyking caused a lowering of the water table to such a critical point, that the drier conditions resulting led to an accentuated ravaging of the forests by fire.

About the beginning of the 1930's, the Secaucus bog was further ditched as a measure of mosquito control. Figure 3 shows the location of the ditches

as well as the effect of ditching on the extent of the bog portion. The area within the solid line which represents the open portion of the bog was not ditched. This bog area was formerly continuous with the upland to the southwest, but after ditching, the ditched area was invaded and covered with *Phragmites communis*. The run-off of fresh water from the upland is partially cut by these ditches, and the existence of the open bog depends a great deal on rainfall. Ditching may have contributed to the death of the last cedars about 1935.

Although fire and the influx of brackish water are largely responsible for the condition of the Secaucus bog, there are a number of associated factors which are also responsible and should be mentioned. Since the turn of the last century, the Hackensack area has become increasingly industrialized. Industrial wastes have been dumped into the creeks and have had much to do with the changing vegetation at Secaucus. The water in Mill Creek has been polluted by the discharge of sewage effluent from the Secaucus disposal plant. Correspondingly, Croma Kill receives the discharges of the disposal plant in North Bergen. Pollution has not only affected the river system, but the air has also been polluted by smoke and poisonous industrial gases. Such conditions have undoubtedly added to the difficulties of existence for cedar. There is also the factor of the amount of fresh water flow in the Hackensack River. This has been reduced as a result of the increase in the use of water by the metropolitan region. This increased utilization of fresh water has resulted in saline tides reaching further up the river. The widening and deepening of the channel of the river has in recent years also allowed for increased flooding by the tides. As a result of the changes brought about by these factors, the plants in the Secaucus bog present today are quite different from those recorded by Torrey in 1819. Only a few of the former bog plants yet remain, and if the present tendency continues these will soon disappear.

Regarding the possibility of cedar again growing in the bog, it seems improbable that it could be able to develop under the present brackish conditions, even barring fire. This is based upon a reference to the salinity of the water in the vicinity of growing cedar in the Cheesequake forest. The evidence obtained in this study is admittedly meager, but is suggestive of long periods of too high salinity at Secaucus. This is related to increased tidal effects and decreased source of fresh water from the nearby upland, both resulting from ditching and decreased flow of fresh water in the Hackensack River. It is also tied up with increased invasion by salt water due to coastal submergence. One is lead to doubt that cedar could exist at the present time under such conditions. However, whether or not it could exist actually requires further study than is presented here.

Coastal submergence has and continues to be a factor of prime importance in the dynamics of this bog. The formation of peat in the bog and in the surrounding marsh is due to rising sea level resulting from the relative change in the level of the land and sea. Marmer (1948) states that this change has been occurring on the Atlantic coast of the United States at about 0.02 foot a year since 1930 and at about one seventh of that rate during a 35 year period prior to that time. If this rise in sea level continues, the bog at Secaucus will eventually be covered by marsh peat. This ultimate condition seems inevitable in the light of past geological history, even aside from the factors induced by human interference.

#### SUMMARY

1. A study of a former southern white cedar bog at Secaucus, New Jersey in the Hackensack tidal marsh is presented. The object of this study was to trace the post-Pleistocene history of the bog and also, to learn what factors have acted to destroy the forest.

2. In gaining this end, an investigation was made of the vegetation, the water salinity, and the underlying peat. As a basis for these studies, three transects were run through the bog and the surrounding marshland. At Cheesequake marsh, 30 miles south of Secaucus on Raritan Bay, another transect was run to study the condition of saline tidal water in relation to a thriving forest of white cedar.

3. Zonation is evident in the marsh vegetation surrounding the bog at Secaucus. *Spartina*, *Typha angustifolia*-*Scirpus olneyi*, *Scirpus olneyi*, and *Phragmites* zones are present. The vegetation of the bog consists of shrubs and scattered deciduous trees, both living and dead, and herbs which have invaded as a result of fire opening up the community and an increased salinity of the water of the bog. Few of the original plants remain.

4. Results of the salinity tests are not conclusive, but suggest that salinity may be a factor in the elimination of cedar from Secaucus.

5. Peat profiles for the three transects show the influence of a rising sea level on the size of the bog. The relative distribution of marsh and forest peat in the profiles indicates an increasingly more limited extent of the bog at higher levels. Forest peat has been and is being overridden by marsh peat. An angiospermous peat layer is evident at the bottom of the profile. Above this, gymnospermous plant remains are present.

6. The post-glacial history is discussed. Following the recession of the ice, glacial Lake Hackensack covered the area. As the land was uplifted, the lake was drained, and the bottom exposed to invading plants. The peat profile reveals *Fraxinus nigra* as one of the first forest species preserved. This species did not persist due to the rise in sea level, but was succeeded by

*Larix laricina* and *Picea mariana* which were favored by the rising water table. These species persisted to the close of the nineteenth century. *Chamaecyparis thyoides* more recently migrated into the bog.

7. The present day vegetation in the bog is quite different from that described by Torrey in 1819. Ditching and fire are the two major factors which have brought about the rapid decadence of the cedar forest today. The rise of sea level has throughout the history of the bog gradually reduced the size of the bog forest. Aside from human interference, it appears that the ultimate fate of the bog is burial in marsh peat.

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THE THREE SUBSPECIES OF *ARISAEMA TRIPHYLLUM*

DONALD G. HUTTLESTON

The purpose of the present brief discussion is to validate, explain and make available to other workers three subspecific names which the writer has used in his unpublished manuscript<sup>1</sup> on *Arisaema* in temperate North America.

After considering the problem of the classification of the American jack-in-the-pulpits from the morphological, ecological and cytological points of view, the author has decided that three populations exist and that these should be treated as subspecies of a single species, namely *A. triphyllum*.

*A. TRIPHYLLUM* subsp. *triphyllum* Huttleston, subsp. nov., based on *Arum triphyllum* L. Sp. Pl. ed. 1. 965. 1753.

Plants with veins of scapes and leaf-sheaths usually not prominent; leaves broad, glaucous beneath; lateral leaflets oblique at bases and moderately to strongly gibbous on outer margins, acutely or obtusely angled at bases; spathe-tubes smooth or obscurely fluted with broad, 2-7 mm., flanges at tops; insides of laminae from wholly green to wholly purple, but usually purple with more or less broad stripes of green or whitish to the tips; growing in dry to moist, shaded locations; somatic chromosome numbers 28 and 56. (The author has made chromosome counts for about 50 plants from various parts of the range. These counts were  $2n = 56$  with the exception of those for two plants collected at Big Gully, Cayuga County, New York, which had  $2n = 28$ . These latter plants could not be separated morphologically from the others.)

Range: In eastern North America from the Gaspé Peninsula and northern Minnesota south to southern Florida and eastern Texas and west to eastern Texas and western Minnesota.

Until recently most botanists thought that this was the variation that Linnaeus had when he described *Arum triphyllum* in his *Species plantarum*. In 1940, Fernald in *Rhodora* stated and gave evidence to support the view that Linnaeus did not have this plant but had what the present writer calls *A. triphyllum* subsp. *pusillum*. After carefully reviewing the evidence, the present author cannot agree with Fernald's conclusion. The specimen in Linnaeus' herbarium which he had marked "4 triphyllum" is definitely a member of this species, but it cannot be assigned to a subspecies since distinguishing characters are not evident. The present writer has not seen the specimen, but a photograph of it appears in *Rhodora* 42: pl. 298. The lateral leaflets are moderately oblique at the bases and the spathe-lamina is pale.

<sup>1</sup> Huttleston, D. G. 1948. A Taxonomic Study of the Genus *Arisaema* in North America. Dissertation, Cornell University.



These are characteristics common to both variations in question. True, the spathe-lamina is narrowly ovate, a condition which, although more common in subsp. *pusillum*, is not infrequent in subsp. *triphyllum*. The flange at the summit of the spathe-tube appears to be rather broad, which is certainly more indicative of the typical subspecies.

In his description, Linnaeus listed three varieties. After a brief description, he designated two other variants beta and gamma. We must assume that the first description alone refers to the typical variant. After this description, which is far too brief for identification, Linnaeus listed four references; Gronovius's *Flora Virginica*, p. 113, Bauhin's *Pinax*, p. 195, *Prodromus*, p. 101, and Dodart's *Memoirs*, p. 81. The first citation, that of Gronovius, reads as follows:

*Arum acaule*, folio ternato.

*Arum minus triphyllum* i. *Arisarum pene viride Virginianum*. Mor. Hist. Oxon. Part III. S. XIII, p. 547. n. 44. T. 5. f. 43.

*Arisarum triphyllum*, pene viride, Banist. Clayt. n. 66.

Since Linnaeus cited the Morrison reference under his variety beta, the only basis that is found in this reference is "*Arum acaule*, folio ternato." which is unidentifiable.

The author, then, must go to the second reference given by Linnaeus. That is Bauhin's *Pinax*, p. 195, and *Prodromus*, p. 101. On page 195 of the *Pinax* is found a very diagrammatic sketch which can be assigned to the species, but not to a subspecies. On page 101 of the *Prodromus*, however, one finds a description which is sufficiently complete to assign it to a subspecies. In the first place, although Bauhin stated that the specimen came from Toupinamboult, Brazil, the plant was actually collected in Canada where subsp. *pusillum* does not grow.<sup>2</sup> In the second place, Bauhin stated that his plant had whitish-green leaves which would indicate glaucescence and the two outer leaflets had a sinus between them on the lower side which would indicate a gibbous condition. Lastly, he stated that the spathe was dark red with whitish stripes through the center. These are all characters of subsp. *triphyllum* as it is here conceived. The fact that the spadix was stated to have been bifid at the summit is not important since plants are occasionally found with compressed and sulcate or even divided spadices.

The last citation given by Linnaeus, that of Dodart's *Memoirs*, p. 81, is even more certainly subsp. *triphyllum*, since he provided an excellent illustration of this subspecies and stated in the description that the leaves were whitish underneath.

*A. TRIPHYLLUM* subsp. *pusillum* Huttleston, comb. nov., based on *A. triphyllum* var. *pusillum* Peck, Rep. N. Y. State Mus. 51: 297, 298. 1899.

<sup>2</sup> Juel, H. O., 1923. Nova Acta Soc. Sci. Upsal. IV. 5: 69-70; and Juel, H. O., 1931. *Rhodora* 33: 175.

Plants with veins of scapes and leaf-sheaths not prominent; leaves light green, but never glaucous, beneath; lateral leaflets moderately to slightly oblique on outer margins and acutely angled at bases; spathe-tubes smooth with flanges 1-2 mm. broad at tops; laminae wholly purple or wholly green, when purple, rarely finely striped with green above the bases; growing in moist to wet woods; somatic chromosome number 28.

Range: From southeastern Connecticut and New York south to central Florida and eastern Texas and west to extreme eastern Texas, eastern Tennessee, southwestern Pennsylvania and eastern New York. In 1931 Nieuwland and Just (Am. Midl. Nat. **12**: 217-220.) described the species *Arisaema deflexum*, from Tamarack Swamp, Turkey Creek Road, Indiana. They reported it to occur in the swamps of the northernmost counties of Indiana and across the boundary in Michigan. Although the author has not seen specimens, he considers it to be *A. triphyllum* subsp. *pusillum*. This would extend the range of the subspecies into the region around the foot of Lake Michigan where a number of coastal plain species have previously been found (see Peattie, D. C., 1922. *Rhodora* **24**: 57-70, 80-88.).

*A. TRIPHYLLUM* subsp. *Stewardsonii* Huttleston, comb. nov., based on *A. Stewardsonii* Britton, Man. Fl. N. U. S. ed. 2. 1057. 1905.

Plants with veins of scapes and leaf-sheaths usually prominent; leaflets narrow, light green, but not glaucous, beneath; lateral leaflets slightly oblique at bases and slightly to moderately gibbous on outer margins, acutely angled at bases; spathe-tubes green with very prominent white flutings or ridges, with narrow or moderately broad flanges, 1-3 mm., at tops; insides of laminae variously marked with purple or purple-brown, most frequently green with purple markings only in the throats, but often purple strongly striped with green, never wholly purple and rarely wholly green; growing in wet, boggy, shaded locations; somatic chromosome number 28.

Range: In northeastern North America from Prince Edward Island, southern Quebec and northwestern New York south and west to western Pennsylvania, northern New Jersey and in the mountains to western North Carolina. One specimen in the Academy of Natural Sciences of Philadelphia was collected by C. C. Deam eight miles east of Michigan City, Laporte County, Indiana, in May, 1932.

Wiegand and Eames in *The Flora of the Cayuga Lake Basin, N. Y.*, p. 134, 135 (1925) mentioned having found plants along the Clyde River southwest of Clyde that were intermediate between *A. triphyllum* subsp. *triphyllum* and subsp. *Stewardsonii*. This author has visited that area and found large numbers of plants growing in low, wet woods which resemble subsp. *Stewardsonii* in habit, leaf-shape, and spathe-tube fluting, but they displayed marked glaucescence on the dorsal surfaces of the leaves. Most of these plants had a character which is not common to either of these subspecies. The two sides of the spathe-tube did not overlap in front but barely met so that a slit was evident in the front of the tube from the top to the base. Despite the fact that subsp. *Stewardsonii* has been characterized by a spreading spathe-tube which forms a V-shaped slit in front, at no other place has the author seen spreading nearly so extreme as in this one loca-

tion. The author has made chromosome counts of six such plants. Two of these had 42 somatic chromosomes and the other four had 28. Specimen number 42 in the Wiegand Herbarium is one of the former plants and numbers 35, 37, and 38 are three of the latter. The author considers this group of plants to have arisen as hybrids between the two subspecies *triphyllum* and *Stewardsonii*. The fact that two of the plants appear to be triploids arising from plants with 28 and 56 somatic chromosomes upholds this opinion. Nothing is known of the fertility of these plants.

**Discussion of the Relationships of Subspecies.** A large number of characteristics have been suggested to separate the three subspecies. This writer has found that most of these criteria, when studied carefully throughout the range, break down and cannot be used as key characters. Below is a discussion of the value of the proposed differences.

**Habitat.** Subsp. *triphyllum* grows in moist, but not wet, locations along watercourses. The other two subspecies are found growing in wet, boggy locations. Occasionally the typical subspecies is found in swamps associated with one or both of the others. Similarly, subsp. *pusillum* and *Stewardsonii* are occasionally found in drier ground near subsp. *triphyllum*.

**Habit.** As a general rule, the typical subspecies is a stout plant whereas the other two are more slender. It is, however, difficult to measure the degree of stoutness and the overlap between the extremes is so great that the character cannot be used as a definite distinguishing point, but it merely contributes to the separations of the subspecies.

**Time of flowering.** Subsp. *triphyllum* is the first to flower in the spring. From one to two weeks after this, subsp. *Stewardsonii* begins flowering and subsp. *pusillum* begins approximately two or three weeks after subsp. *triphyllum* has begun. It is not unusual, however, to find all three in flower at the same time since each of them continues flowering for a number of weeks.

**Leaf color.** Subsp. *Stewardsonii* tends to have dark green leaves while the leaves of the other two subspecies are lighter. Only the typical variant shows glaucescence on the dorsal surfaces of the leaves and in these plants it is very marked when the leaves are mature. Although the leaves of the other two subspecies are somewhat lighter beneath, they are not glaucous. As has been pointed out under the discussion of subsp. *Stewardsonii*, in a location southwest of Clyde, New York, numerous specimens, which were otherwise this subspecies, do show glaucescence. It is very possible that other locations will be found where this is the case.

**Leaf shape.** The leaflets of subsp. *triphyllum* tend to be broadly ovate or obovate whereas those of both other subspecies tend to be narrowly ovate or lanceolate. There is considerable overlap in this respect. The lateral leaflets of the first variant are usually strongly gibbous on the outer margins and

obtusely angled at the bases. Those of the other two subspecies are never strongly gibbous or obtuse at the bases, but are moderately to slightly gibbous and narrowly to moderately acute. Considerable gradation is displayed here also.

*Spathe-lamina color.* The coloration of the insides of the spathe-laminae varies from unmarked purple through various degrees of striping with green or whitish to unmarked light green. Those of the typical subspecies cover the entire range of variation, but are very rarely wholly purple and are usually purple marked with prominent green or whitish stripes from the base to the tip. Those of subsp. *Stewardsonii* are never wholly purple and approximately 75 per cent are green, more or less marked with purple between the veins in the throats only. Occasionally plants of this group are found which have unmarked green spathe-laminae and they are commonly purple, prominently striped with green. Nearly all of those of subsp. *pusillum* are wholly purple with stripes evident only at the bases or unmarked green in about a 3:1 ratio respectively. Occasionally a plant is found with narrow, green stripes on the purple lamina. In these, most frequently, the one stripe follows the central vein. Inasmuch as all the color phases displayed by one subspecies can be found in one colony with one coloration grading imperceptibly into another, it seems impractical to affix names to them. This author feels that the use of the terms "the striped variety," "the purple variety," or "the green variety" will suffice.

*Spathe-lamina shape.* It has been suggested that the shape of the spathe-lamina can be used to separate the subspecies. Here again, there is a tendency toward a separation, but the degree of variability and the overlapping make the character of questionable value. That of subsp. *pusillum* tends to be narrowly ovate with a long acuminate tip. That of subsp. *triphyllum* tends to be ovate with a short acuminate or acute tip and that of subsp. *Stewardsonii* tends to be broadly ovate with a short acute tip.

*Spathe-tube flange.* The breadth of the flange or deflexed portion at the top of the spathe-tube is fairly good as a separation character. Subsp. *triphyllum* has a broad flange, 2-7 mm. Subsp. *Stewardsonii* has a moderate flange, 1-3 mm., and subsp. *pusillum* has a very narrow flange, 1-2 mm. Actual measurements cannot be used since the flange of a small plant of the first might be narrower than that on a large plant of the last.

*Spathe-tube.* The fluting of the spathe-tube is the best character for separating subsp. *Stewardsonii* from the other two. The tube in that subspecies is always very strongly ridged or fluted whereas in the other two it is obscurely fluted, if at all. Wiegand and Eames (Fl. Cayuga Lake Basin 134 & 135. 1925.) characterized subsp. *Stewardsonii* as having a V-shaped opening between the margins of the tube at the top. This character does not hold throughout the range of the subspecies.

*Spadix shape.* The spadix of *A. triphyllum* subsp. *triphyllum* is more or less clavate whereas the spadices of subsp. *pusillum* and *Stewardsonii* are cylindric or subcylindric. The difference, however, is too fine to be of much value.

*Seed shape.* Prof. M. L. Fernald (*Rhodora* 42: 247-253 *ill.* 1940.) proposed a seed character as a separation point. He stated that seeds of subsp. *pusillum* and *Stewardsonii* were invaginated at the base around the hilum, whereas those of subsp. *triphyllum* were not. This author has not been able to demonstrate any correlation in this characteristic.

*Chromosome number.* This author has made about fifteen chromosome counts of subsp. *Stewardsonii* and seven of subsp. *pusillum* and found them to be  $2n = 28$ . Of about 50 counts made by the author on subsp. *triphyllum*, all except two were  $2n = 56$ . The two exceptions were  $2n = 28$  and both specimens were collected by the writer in Big Gully, Cayuga County, New York. Atkinson (*Bot. Gaz.* 28: 1. 1899.) reported the gametic number of *A. triphyllum* as 16 and Bowden (*Am. Jour. Bot.* 27: 357-371. 1940.) reported the species to have 56 somatic chromosomes. Since no specimens are available, it is impossible to ascertain from what subspecies these counts were made.

In this author's opinion, a mere difference in chromosome number, particularly the difference between diploid and tetraploid, is not adequate reason for the erection of separate species. In addition there must be sufficient morphological difference between two populations of plants to render any given plant assignable to one or the other species. Even though several characteristics contribute to the separation of these three populations, most of these characters are quantitative and it is frequently difficult or impossible, particularly with pressed specimens, to assign individual plants to one population. True, a tetraploid should not be expected to hybridize freely with a diploid, but this author has found two specimens of the tetraploid subspecies *triphyllum* at Big Gully, Cayuga County, New York which had  $2n = 28$  chromosomes. It is very possible that these diploids are considerably more common than these findings would indicate. In the case of subsp. *pusillum* and *Stewardsonii* only quantitative characters serve to separate the two. Even though the two populations are partially separated geographically, this writer has found one swamp at Clintondale Station, Ulster County, New York where both subspecies grow together with a number of intermediates. It is felt that the separations between these three populations are something less than those required between species, and thus the populations have been described as subspecies.

It is very probable that the three subspecies arose from one original population in North America. The question of how they arose, on the other

hand, is not as easy to answer. Two interpretations appear to be indicated. In the first place, the original population could have split into two, subsp. *Stewardsonii* which was hardier and spread north and subsp. *pusillum* which spread south. At one time a hybrid arose between these two and its chromosome number was or became doubled resulting in an allotetraploid. If this is the explanation, it is to be expected that the tetraploid would combine the characters of the two diploids. When one analyzes the characteristics of the three subspecies, it is immediately evident that this is not the case. The tetraploid, *A. triphyllum* subsp. *triphyllum*, in the characters of habitat, habit, time of flowering, leaf shape and width of spathe-tube flange falls, not between the other two subspecies, but to one side of both of them. It is true that these characters might be thrown out as being due to the increased vigor of the tetraploid, but it would be difficult to explain away the glaucescence of the leaf and the clavate shape of the spadix on this basis. The other interpretation which seems to be indicated, and the one which is favored by this author, is that the original population gave rise to three separate populations and that the chromosomes in one of them were or became doubled. This tetraploid, then, being more vigorous, spread more rapidly and widely than the diploids. This interpretation would allow for the presence of the characteristics of the tetraploid which differ from those of either of the other subspecies. The presence of diploids which apparently cannot be separated from the tetraploids would be further proof of this interpretation.

#### SUMMARY

A study has been made of the eastern American jack-in-the-pulpits that have, in the broad sense, been considered as *Arisaema triphyllum*. These comprise a single species consisting of three major races. One of these races is widespread in eastern North America and, seemingly, predominantly tetraploid. The two others are diploid and more restricted in range. Of these, one is essentially northern and upland; the other is essentially southern and coastal. A sufficient degree of overlapping in the morphological characters has been found to support the treatment of these three races as subspecies, rather than full species. Restudy of the elements concerned in the original publication of *Arum triphyllum* L., the basonym of *Arisaema triphyllum*, indicates that the widespread tetraploid should be considered as the typical element and it is here designated as subsp. *triphyllum*. The other two subspecies are designated as subsp. *Stewardsonii* and *pusillum*. It is considered most probable that these three races arose from a common stock, with subsequent geographical and ploidal divergence of morphological types.

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CYTOLOGICAL EVIDENCES OF HYBRIDIZATION BETWEEN  
JUNIPERUS VIRGINIANA AND J. HORIZONTALISJAMES G. ROSS<sup>1</sup> AND ROBERT E. DUNCAN<sup>2</sup>

Colonies of presumed interspecific hybrids within the genus *Juniperus* have been observed by Fassett (1944 b, 1945 a, 1945 b,) in certain areas where the geographic ranges and ecological habitats of two species overlap. On the eastern edge of the Driftless Area of Wisconsin, and along the coast of Maine, colonies composed of individuals with characteristics intermediate between those of *Juniperus virginiana* L. and *J. horizontalis* Moench have been observed. In general the range of *J. virginiana* lies southward and that of *J. Horizontalis* to the north of these regions (Fassett 1945 b). Except in the areas of overlap, each of the species has a characteristic combination of characters. More information on the nature of individuals in colonies situated in such regions has now been sought through a cytological investigation.

**Materials and Methods** The colonies selected for studies of the presumed hybrids were those occurring within the eastern fringes of the Driftless Area in southwestern Wisconsin. Identifications of presumed hybrids were made by the method described by Fassett (1945 b). The locations of these colonies, as well as those of the putative parental species which were investigated, are indicated on a map of northeastern U.S.A. (fig. 1).

Preparations suitable for the study of somatic metaphase chromosomes were obtained from tissue of immature leaves or cones treated for 3-4 hours in a saturated aqueous solution of paradichlorobenzene before fixation in acetic alcohol (1 : 3) for one half hour longer. After hydrolysis in 1N HCl for 8 minutes at 60° C, the material was stained in aceto-carmin.

Meiosis was studied in pollen mother-cells from male cones collected during July and August, 1946. Good fixation of this material was not the rule. Of the killing agents used (Carnoy's, Fleming's, and Craf) a modification of Carnoy's fixative (6 abs. alcohol : 2 glacial acetic acid : 1 chloroform) was found superior though not dependable. The aceto-carmin squash technique gave the most satisfactory preparations. Meiosis in *J. horizontalis* was found to occur from the middle to the end of July and in *J. virginiana* from the

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middle to the end of August, while in most of the individuals in the hybrid colonies it occurred in the intervening time. A comparative measure of irregularity at meiosis for each individual was obtained by inspecting 100 pol-

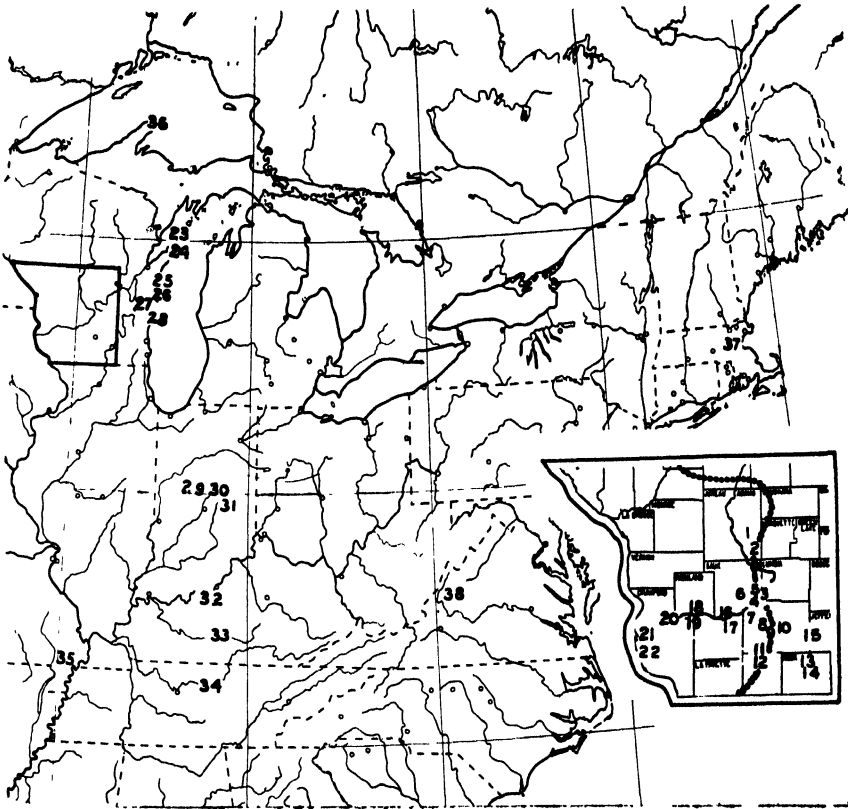
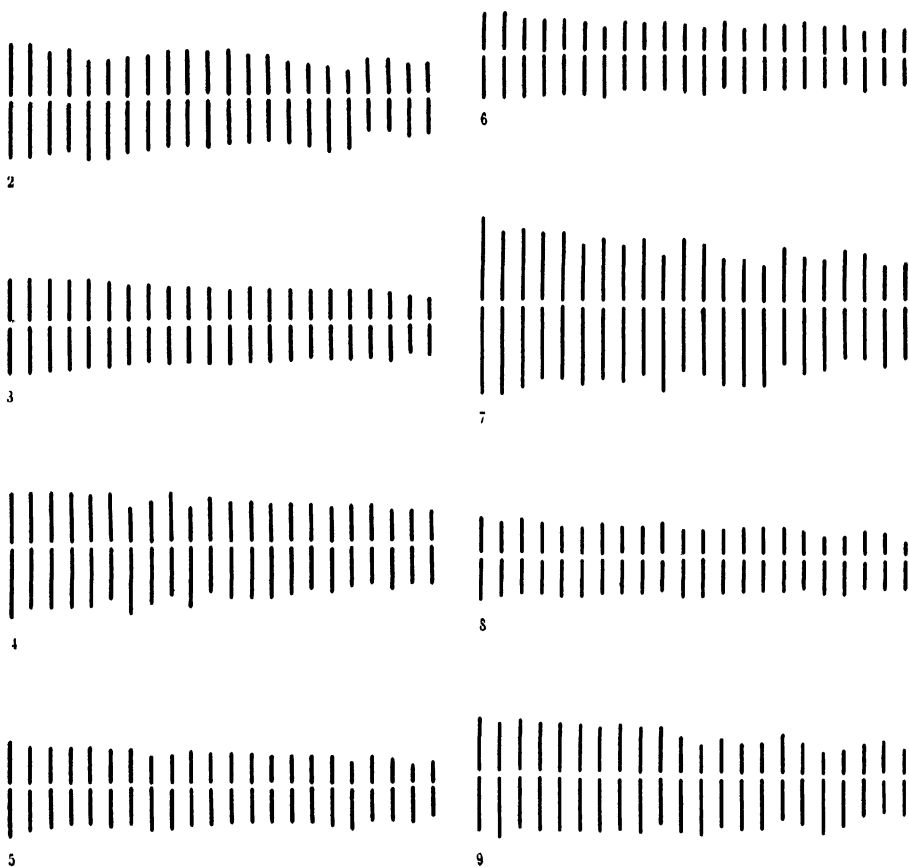


FIG. 1. A map of northeastern United States with an inset of a portion of Wisconsin indicating with a dotted line the eastern limits of the unglaciated Driftless Area. The general locations studied are indicated. *J. virginiana* Colonies: Numbers 3—Okee, Wisconsin; 5—Prairie du Sac, Wisconsin; 6—West of Sauk Prairie, Wisconsin; 7—Mazomanie, Wisconsin; 10—Madison, Wisconsin; 13—Edgerton, Wisconsin; 14—Janesville, Wisconsin; 15—Hope Lake Bog, Wisconsin; 16—Spring Green, Wisconsin; 17—Tower Hill Park, Wisconsin; 18—Sauk City, Wisconsin; 19—Muscola, Wisconsin; 20—Boscobel, Wisconsin; 21—Prairie du Chien, Wisconsin; 22—Bagley, Wisconsin; 29—Lebanon, Indiana; 30—Indianapolis, Indiana; 31—Pendleton, Indiana; 32—Fort Knox, Kentucky; 33—Mammoth Onyx Cave, Kentucky; 34—Gallatin, Tennessee; 35—Bloomsdale, Missouri; 37—Boston, Massachusetts; 38—Lexington, Virginia. *J. horizontalis* Colonies: Numbers 23—Sister Bay, Wisconsin; 24—Bailey's Harbor, Wisconsin; 25—Point Beach State Park, Wisconsin; 26—Two Rivers, Wisconsin; 27—Elkhart Lake, Wisconsin; 36—West Bluff, Keweenaw Point, Michigan. Presumed hybrid Colonies: Numbers 1—Sec. 33-T.17N-R.6E, Wisconsin; 2—Grand Marsh, Wisconsin; 4—Black Hawk Lookout, Wisconsin; 8—Black Earth, Wisconsin; Cross Plains, Wisconsin; 9—Pine Bluff, Wisconsin; 11—Belleville, Wisconsin; 12—New Glarus, Wisconsin.





FIGS. 2-9. Ideograms representing the chromosome sets of individuals of the putative parents and presumed interspecific hybrids between *J. horizontalis* and *J. virginiana*. 1020 x. Figure 2. *J. horizontalis*. Figure 3. *J. virginiana*. Figures 4-7. Individuals from the presumed hybrid colony at Pine Bluff. Figures 8-9. Individuals from the presumed hybrid colony at New Glarus.

len mother-cells at the two-nucleate or four-nucleate stage; or, if a study of meiosis could not be made, 400 immature pollen grains were examined.

Collections of male cones containing almost mature pollen were made during the last part of February and the first part of March in 1947. Samples of pollen grains from each of five cones from each individual were stained with aceto-carmin and the number of grains with normal appearance expressed in per cent of the total.

**Observations** The somatic chromosome numbers of individuals of both species as well as their presumed hybrids were found without exception to be 22. Somatic chromosomes of *J. virginiana* and *J. horizontalis* (illustrated in figures 10 and 11 respectively) are very similar. A somewhat heterobrachial pair among the chromosomes of *J. horizontalis* distinguishes its ideogram (fig. 2) from that of *J. virginiana* (fig. 3). The ideograms in figures 2-9 represent chromosome complements of the plants studied, with the chromosomes arranged in decreasing length from the left with short arms uppermost. The unbalance observed within the chromosome complements of the presumed hybrids (figs. 4-9) is occasioned by heterobrachial chromosomes without counterparts. This unbalance distinguishes the chromosome sets of the presumed hybrids from those of their putative parents.

Differences in chromosome lengths were observed between cells examined within the one tissue after treatment with paradichlorobenzene. The shortening is presumably a function of the length of time which the chromosomes have been at metaphase. Except in the case of figure 7, the difference between ideograms in total chromosome length may be attributed to this factor. The length of the chromosomes represented in figure 7 may be taken as the norm since the tissue from which these measurements were made was untreated.

The degree of irregularity occurring at meiosis in the taxonomically acceptable members of both putative parents was first investigated. Pairing proceeded normally during prophase and subsequent irregularities were few. The total number of chiasmata observed at metaphase of both species varied from 21 to 24 per pollen mother-cell. With the exception of a bridge-fragment configuration (fig. 21) observed in an individual of *J. horizontalis*, the only type of irregularity noted was the presence of micronuclei or their precursors, lagging chromosomes. In table I the average percentages of irregularities at meiosis are indicated for a number of plants of both the species and presumed hybrids.

Members of the New Glarus and Pine Bluff colonies, both located on sandstone hillsides, were selected for detailed study of the presumed hybrids. At New Glarus all plants were creeping with the exception of one upright individual. Other specific characters, however, occurred in apparently ran-

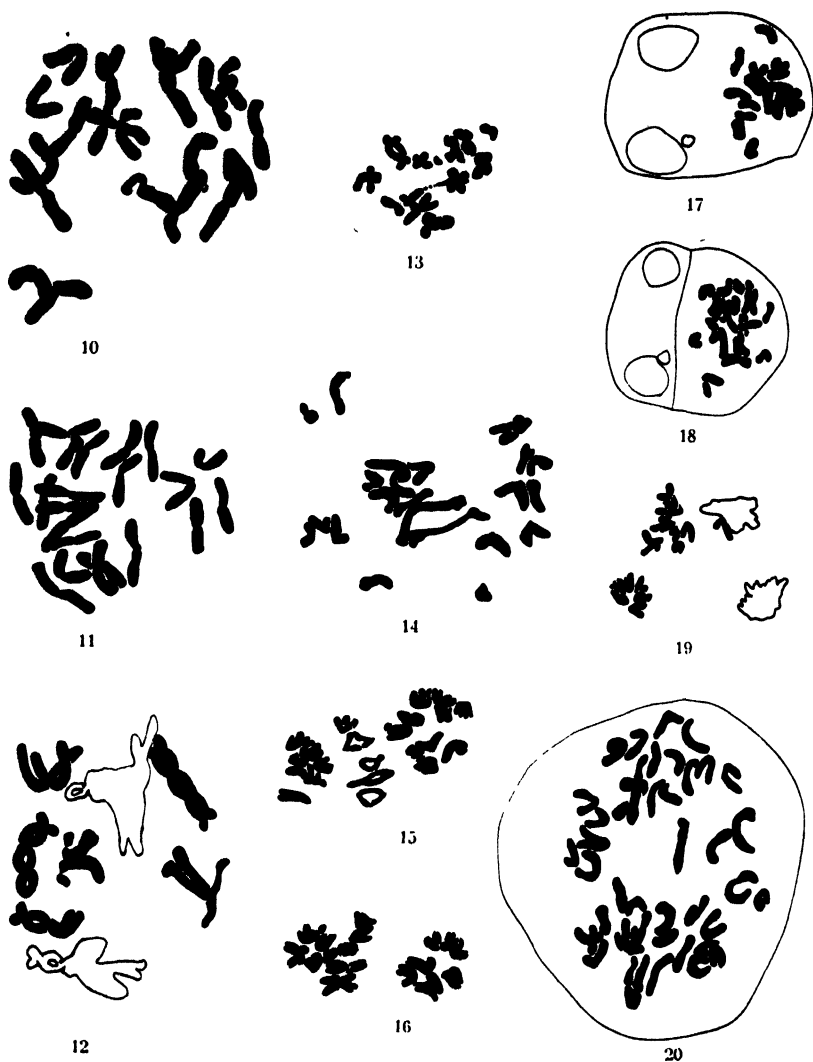


FIG. 10. Somatic chromosomes of *J. horizontalis* from Colony number 27, 970  $\times$ . FIG. 11. Somatic chromosomes of *J. virginiana* from Colony number 10, 970  $\times$ . FIG. 12. Diakinesis in a presumed hybrid from the Pine Bluff colony showing two associations which could not be interpreted, 970  $\times$ . FIG. 13. Anaphase I in a presumed hybrid from the New Glarus colony showing a bridge and fragment as well as two unpaired chromosomes, 610  $\times$ . FIG. 14. Anaphase I in a presumed hybrid (New Glarus plant number 6), indicating the occurrence of unpaired chromosomes and also two bridge-fragment configurations, 970  $\times$ . FIG. 15. Anaphase I in a presumed hybrid (New Glarus plant number 6), showing univalents dividing at the equator, 610  $\times$ . FIG. 16. Anaphase I in a presumed hybrid (New Glarus plant number 6), showing 8 chromosomes at one pole and 14 at the other, 610  $\times$ . FIG. 17. Second meiotic division in a presumed hybrid (New Glarus plant

dom combinations. The colony at Pine Bluff contained individuals with all specific characters occurring in apparently random combinations. More meiotic irregularities were found in members of the New Glarus colony than in those at Pine Bluff. In a semi-erect plant at Pine Bluff (plant number 23) nearly all sporangia were aborted, while the remainder contained clumped pollen mother-cells abnormal in appearance. It is not included in table I.

TABLE 1. *Average percentage of cytological irregularities observed at microsporangogenesis in the species and their presumed hybrids.*

	<i>J. virginiana</i> (4 colonies) <sup>1</sup>	<i>J. horizontalis</i> (3 colonies) <sup>2</sup>	Presumed hybrids	
			New Glarus (Colony no. 12)	Pine Bluff (Colony no. 9)
Total no. plants examined	11	8	6	10
2-nucleate p.m.c.'s:				
No. individuals examined	8	8	5	9
Average no. p.m.c.'s examined	252	313	243	268
Mean percentage irregularity	0.19	0.32	5.56	1.54
Range of percentages	0-0.91	0-1.90	1.00-20.00	0-12.50
4-nucleate p.m.c.'s:				
No. individuals examined	9	8	6	10
Average no. p.m.c.'s examined	281	460	335	350
Mean percentage irregularity	0.02	0.24	20.10	1.00
Range of percentages	0-0.22	0-1.18	0.98-56.62	0-6.50
Immature pollen:				
No. of individuals examined	10	3	2	1
Average no. p.m.c.'s examined	1509	598	1024	440
Mean percentage irregularity	0.05	0.24	7.55	0
Range of percentages	0-0.41	0.20-0.32	6.96-8.14	0

<sup>1</sup> Lexington, Virginia; Madison, Wisconsin; Bagley, Wisconsin; Prairie du Chien, Wisconsin.

<sup>2</sup> Two Rivers, Wisconsin; West Bluff, Keweenaw Point, Michigan; Terry Andrae State Park, Wisconsin.

In members of the Pine Bluff colony, bridge-fragment configurations, lagging chromosomes and micronuclei were observed at the two-nucleate stages.

number 6) showing lack of coincidence of the two divisions, 610 $\times$ . FIG. 18. Second meiotic division in a presumed hybrid (New Glarus plant number 13) showing a lack of coincidence of divisions and also a cell wall between the two sides, 610 $\times$ . FIG. 19. Anaphase II in a presumed hybrid (New Glarus plant number 6) showing 7 chromosomes at the one pole and 10 chromosomes at the other, 610 $\times$ . FIG. 20. Anaphase II in a presumed hybrid (New Glarus plant number 6) showing non-orientation of the chromosomes, 970 $\times$ .



The percentage of these irregularities varied between individuals. At diakinesis a semi-prostrate plant at Pine Bluff (plant number 26) had in most cases 4-6 bivalents, and generally two other associations containing the rest of the chromosomes (fig. 12). These multiple associations usually resolve into pairs at metaphase though occasionally there is an apparent connection between different bivalents (fig. 23). The number of contact points that may be counted as chiasmata in the metaphase chromosomes of this plant varied from 18 to 23 per pollen mother-cell. In some cases, both in this plant and in others, two unassociated chromosomes were observed at metaphase I (fig. 24). Structural heterozygosity was also indicated by the observation of bridges at first anaphase (fig. 22).

Associations of groups of bivalents at prophase were seen less frequently in pollen mother-cells of individuals from the New Glarus colony, but, again, structural heterozygosity was indicated by the occurrence of bridge-

TABLE 2. *Distribution of chromosomes at first anaphase in pollen mother-cells of New Glarus plant no. 6.*

Distribution Categories					
0-22	1-21	2-20	3-19	4-18	5-17
0	0	0	2	1	3
Distribution Categories					
6-16	7-15	8-14	9-13	10-12	11-11
1	2	6	2	2	2

fragment configurations (figs. 13 and 14) and the presence of laggards at anaphase I and II. In some cells of a creeping individual at New Glarus (plant number 6) laggards were observed to be dividing at anaphase I (fig. 15), while in others, their division presumably took place at anaphase

FIGS. 21-29. Photomicrographs of meiosis in one putative parent and in presumed hybrids of *Juniperus horizontalis* and *J. virginiana*, 1020 $\times$ . FIG. 21. Anaphase I in *J. horizontalis* showing a bridge and fragment. FIG. 22. Anaphase I in a presumed hybrid (Pine Bluff plant number 26) showing a bridge. FIG. 23. Metaphase I in a presumed hybrid (Pine Bluff plant number 26) showing 11 bivalents with an arrow pointing to what appears to be an association between two bivalents. FIG. 24. Metaphase I in a presumed hybrid (Pine Bluff plant number 26) showing two unpaired chromosomes. FIG. 25. Telophase I in a presumed hybrid (New Glarus plant number 6) showing three lagging chromosomes which do not appear double and therefore may divide during the second division. FIG. 26. Metaphase I in a presumed hybrid (New Glarus plant number 6) showing almost complete lack of association of the chromosomes. FIG. 27. Interkinesis in a presumed hybrid (New Glarus plant number 6) illustrating a gross difference in size of the polar groups. FIG. 28. "Tetrad" stages in a presumed hybrid (New Glarus plant number 6) showing different nuclear sizes. FIG. 29. "Tetrad" stages in a presumed hybrid (New Glarus plant number 6) showing different nuclear sizes. FIG. 29. "Tetrad" stages in a presumed hybrid (New Glarus plant number 6) showing super-numerary nuclei.

II (fig. 25). In many cells most of the chromosomes were unassociated at metaphase I (fig. 26) and the total number of chiasmata was in many cases as low as 7 or 8. Examination of pachytene, however, indicated no unpaired strands. Unequal distribution was often noted at anaphase I. In figure 16 there are 14 chromosomes at one pole and 8 at the other. Only two anaphase I figures out of the 21 examined on this same slide had 11 chromosomes at each pole. All distributions other than 0:22, 1:21, 2:20 were found (table II). The pronounced difference often noted in size of the two groups is illustrated in figure 27.

TABLE 3. Percentages of apparently normal pollen of the species and their presumed hybrids.

Classification	Total no. of Plants	Mean no. Examined per Plant	Mean per Cent with Normal Appearance	Range of Percentages
<i>J. virginiana</i> (21 colonies)	80	602	98.1	88.5-100
<i>J. horizontalis</i> (7 colonies)	24	579	99.2	95.0-100
Colonies of Presumed Hybrids				
New Glarus (Colony No. 12)	10	551	79.9	59.5-94.5
Pine Bluff (Colony No. 9)	20	870	87.1	46.0-99.5
Belleville (Colony No. 11)	8	537	94.9	75.0-100
Black Earth (colony No. 8)	8	827	97.4	91.5-100
Grand Marsh (Colony No. 2)	6	500	98.5	97.5-99.5
S 33-T17N-R6E (Colony No. 1)	3	500	98.5	97.0-99.0
Cross Plains (Colony No. 8)	7	1004	98.6	97.0-99.5
Blk. Hawk Lkt. (Col. No. 4)	3	500	99.3	99.0-99.5

At the four-nucleate stage most of the irregularities in members of both the Pine Bluff and New Glarus colonies consisted mainly of laggards or micronuclei. Unequal distribution noted in certain members of the New Glarus colony at anaphase II, (fig. 19), may result in two large and two small nuclei similar to those shown in figure 28. In some cases (fig. 20), almost complete disorientation of the chromosomes was found at division II. These clumps of chromosomes would presumably later form many nuclei of varying sizes as shown in figure 29. Lack of coincidence of the second nuclear divisions was often observed in some individuals of the New Glarus colony (figs. 17 and 18). A cell wall was sometimes found between the nuclei in the binucleate stage (fig. 18) while at other times it is lacking until after

the four-nucleate stage is reached, at which time the cross walls are formed concurrently.

Examinations of immature pollen of two individuals in the New Glarus colony disclosed a great number of pollen grains with micronuclei. Some pollen grains contained two nuclei, others were aborted or minute. Immature pollen was examined from only one individual at Pine Bluff; no irregularities were observed.

The percentages of apparently normal pollen, indicated in table III, were found to be high in individuals of both species. Certain individuals of *J. virginiana* had lower percentages of apparently normal pollen than any plant of *J. horizontalis* but the mean percentages, 98.1 for the former and 99.2 for the latter, differed by only 1.1%.

The pollen of certain individuals which on morphological grounds were presumed to be of hybrid origin, contained considerably more defective grains than were observed in any individual of the putative parent species. For example, two individuals in the New Glarus colony were observed to have only 59.5% apparently normal pollen. Though the mean percentage is higher for individuals in the Pine Bluff colony, the range extends lower than for individuals in the New Glarus colony. Individuals in other presumed hybrid colonies showed little evidence of defective pollen. The most heterogeneous colonies, namely New Glarus and Pine Bluff, Fassett (1945 a), were found to have considerably lower averages of good pollen than either of the species or any of the more homogeneous presumed hybrid colonies.

**Discussion** On taxonomic evidence presented by Fassett (1945 b), and substantiated by this study, heterogeneous colonies occurring in the Driftless Area of Wisconsin may be presumed to be either the variable progenitors from which these two species have stemmed or they may be hybrids originating from the meeting of the two species owing to an overlap of their ecological habitats. A measure of credibility could be given the former since it is believed that certain elements of the flora in the Driftless Area survived the various glacial periods, but Fassett (1945 b) has described similar colonies on the coast of Maine where the ranges of the two species overlap in an area known to be entirely glaciated. The hypothesis that these colonies are of hybrid origin therefore appears to be the more probable. The cytological data collected in this study favor further the assumption of hybridity.

The one pair of chromosomes that is distinctly heterobrachial in the complement of *J. horizontalis* should be recognizable among the chromosomes of an  $F_1$  hybrid of this species with *J. virginiana*, which has no heterobrachial chromosomes. Since these chromosomes could not be identified with assurance in the sets of the presumed hybrids examined, it is possible



that these plants may be backcross progeny to *J. virginiana* or of later hybrid generations. The presence of other heterobrachial chromosomes without counterparts was noted in the ideograms of the presumed hybrids. These may have originated through crossing over within homologous areas situated in different parts of the members of a bivalent, or through aberrancies such as have been observed in the presumed hybrid material caused by crossing over within inversions or translocations. Emsweller and Jones (1938) have reported the occurrence of different morphological types of post-meiotic chromosomes in the interspecific hybrid *Allium cepa*  $\times$  *A. fistulosum*. They consider these "new" chromosomes to be formed by crossing over between the two genomes as postulated here.

The unpaired chromosomes seen in varying numbers at different metaphases of pollen mother-cells of some individuals at New Glarus may indicate that the homology of their chromosomes is less than that observed in the species. The almost normal pairing observed at pachytene indicates that the unpaired chromosomes at metaphase are desynaptic rather than asynaptic. Pairing of nonhomologous chromosomes has been observed by McClintock (1933) in maize, and also by Levan (1942, 1945) in haploid rye and haploid sugar beets. The possibility of all so-called "asynaptic" chromosomes being actually the result of desynapsis is suggested by Li, Pao and Li (1945) but Huskins and Wilson (1938) show that in *Trillium* two types of asynapsis as well as desynapsis can be differentiated when the coiled chromonemata with their changes of direction can be analyzed. This is not possible in *Juniperus*. Andersson (1947) states that the "asynaptic" chromosomes which he found in *Picea abies* were observed to be paired at pachytene and to separate gradually as the prophase progresses. The types of aberrancies reported by him are somewhat similar to those reported in this study though he found unpaired chromosomes in greater numbers. Evidence of structural hybridity was not observed and the "asynaptic" condition was attributed to genetic causes. The taxonomic characters of the asynaptic spruce were typical of the species as were also those in the same colony. Whether the occurrence of unpaired chromosomes at first metaphase of meiosis in New Glarus plant number 6 is gene-determined or due to the lack of homology of the chromosomes cannot be ascertained from the facts at hand. If the latter, the hybrid nature of these plants is strongly indicated.

The difference in timing occasionally noted in the division process of different nuclei within pollen mother-cells of New Glarus individuals was also noted to a slight degree in an individual of *J. horizontalis*. Either a mechanical or genic change in the chromosomal constitution may be responsible for disturbing the equilibrium of the meiotic process.

The effect of environment on the meiotic process cannot be discounted

when sterility phenomena are being considered. Pine Bluff plant number 23, which contained aborted sporangia in the male cones, was somewhat shaded by an oak tree growing nearby. As early as 1908 Tischler found that lack of light caused the formation of a high proportion of bad pollen in two species of *Potentilla* and in their hybrid it caused complete sterility. He maintained that the effect of lack of light in causing pollen sterility was disproportionately greater on the interspecific hybrids than on the species. As shown in extensive studies by Oehlkers (1937) the general physiological state of the plant is reflected in the number of chiasmata formed at prophase. The abortion noted in Pine Bluff plant number 23 may have been at least partly a result of shading. Shading could not have been responsible for the sterility noted in the New Glarus colony, since these plants were in a favorable position on an open hillside. The low number of chiasmata and the many unpaired chromosomes observed in pollen mother-cells of New Glarus number 6 probably may be attributed to causes other than environment.

Differences in levels of pollen fertility and in degrees of irregularity at meiosis between presumed hybrid colonies may be an indication of the age of the colony. Irregularities at meiosis would tend to be eliminated during sexual reproductions since only gametes with a balanced genic constitution would be viable. Therefore, such colonies as those at Black Earth and Cross Plains which appear to have little or no pollen sterility, may have originated many generations ago, and have spread from the point of hybridization throughout the surrounding area. In some isolated colonies all individuals have certain characters of one or the other of the species, while the other characters occur at random. The large amount of pollen sterility and the high percentage of meiotic irregularities noted in New Glarus individuals may indicate that this colony is the progeny of recent hybridizations. Two trees with the characteristics of *J. virginiana* were noted in that vicinity as were also individuals with the taxonomic features of *J. horizontalis*. The absence of individuals with intermediate growth habits cannot be explained on the premise of recent hybridization, unless it is supposed that the creeping habit is dominant and the individuals are all  $F_1$ . It is possible, though unlikely, that some selective force may favor the creeping individuals and prevent the appearance of the semi-prostrate habit. This colony could also conceivably be the progeny of a back-cross of an  $F_2$  or  $F_3$  individual to *J. horizontalis*, but the low fertility observed makes this hypothesis improbable.

The small number of individuals intermediate between the two species growing side by side on the hilltop and hillside at Grand Marsh, may be explained by postulating as does Fassett (1945 b) that at this point some internal barrier exists between the species. The normal appearance of the pol-

len of these intermediate types may indicate that they are the successful progeny of an ancient hybridization, but the possibility that they may be  $F_1$  progeny cannot be discounted since normal pollen has been reported in the  $F_1$  of species crosses (Huskins 1929). Different strains of the same species may give species hybrids of quite different behavior as previously discussed. Likewise, the internal barrier to hybridization which may exist between the individuals of the species at Grand Marsh may not be present in other strains of these species. A somewhat similar situation may exist at Elkhart Lake, Wisconsin, (colony number 27) which conformed taxonomically to *J. horizontalis*. The presence of berries with seeds was noted on the female individuals, which as far as could be determined could have received pollen only from *J. virginiana*. Though seeds were found to be set, no intermediate individuals occurred in the vicinity.

Since the colony at Pine Bluff was initially selected as the critical material for this study, corresponding pollen and meiotic studies were made on the same trees. The percentage of apparently normal pollen was not always what might be expected through an examination of the meiotic process. In some plants meiosis was regular and pollen appeared normal, in other trees meiosis was regular and yet considerable pollen was aborted, and in another case meiosis was somewhat irregular but the pollen appeared normal. Variability in the amount of apparently normal pollen among cones was found and it may be possible that, since in certain cases the pollen sample was taken from a different part of the tree than was the sample for meiosis, the discrepancy may be due to environmental effects. In cases where no irregularities were observed at meiosis and yet there was a great deal of pollen abortion, minute structural losses within the chromosomes may be responsible. The occurrence of a high percentage of good pollen after the observation of irregularities at meiosis cannot so readily be explained unless environmental effects may be operative in producing the latter. It is possible also that, though appearing normal, the pollen would carry deficiencies or duplications which would cause it to be nonfunctional. Peto (1938) also found in poplar hybrids apparently normal pollen from an individual whose meiosis was quite irregular. Closer examination disclosed minute debris which he interpreted as being aborted pollen grains. In the pollen from the plant under discussion here, however, such debris was not evident. In Pine Bluff plant number 23, there seems to have been abortion of pollen mother-cells before meiosis. The percentage of apparently normal pollen was considerably higher than might have been expected from the clumped pollen mother-cells observed in young sporangia. It is quite possible that some of the less sterile cones owe their greater fertility to a more fortunate situation with regards to light, translocation of food, temperature at a critical period, or to any of a variety of physiological factors.

As stressed by Huskins (1929) each one of the points concerning evidence for hybridity could be refuted if offered alone as a criterion. The appearance of chromosomes morphologically dissimilar to those of both species could be explained by supposing losses, inversions, and translocations of chromosome parts which may occur within one species. In fact, evidence of an inversion was found within *J. horizontalis* but neither was the meiotic process greatly disturbed nor did the pollen fertility appear reduced. "Asynapsis" controlled by a genetic factor has been observed in a number of species as has also pollen sterility. In addition, certain environmental influences may cause aberrancies resembling these irregularities. Even the sum of these cytological observations by themselves cannot be accepted as proof of hybridity but in conjunction with the taxonomic data the validity of this assumption is strengthened.

The length of time that would be involved in making a cross between these species and in studying their progeny, as recommended by Baker (1947), makes the experimental approach impracticable. Strains within the species may differ in their ability to cross. Such incompatible strains may be present at Elkhart Lake and at Grand Marsh. This points out a weakness in the experimental approach since failure to make a cross artificially may not mean that its occurrence is impossible in nature.

The extent of gene flow from these centers of hybridization does not seem to be great. At Pine Bluff the hybrid colonies are limited to the neighboring hillsides. An occasional presumably hybrid colony exists along the side of the valley between Cross Plains and Black Earth. There, the flow of genes of *J. horizontalis* into *J. virginiana* seems to have ended. Southward from Pine Bluff evidences of hybridization are found at Belleville and at New Glarus.

The competition afforded these hybrid forms by the species may account for their limitation to different area. The species are particularly adapted to the ecological habitats in which they are found and so would tend to prevent the spread of hybrid forms which probably would be less well adapted. These hybrid colonies, however, can be regarded as a reservoir from which gene flow may be expected if change of environment were to occur.

**Acknowledgements** The authors wish to thank Dr. N. C. Fassett for suggesting this problem and for his help in collecting material and in making taxonomic classifications. They also wish to thank Dr. C. L. Huskins for general criticisms and help in interpreting certain cytological figures.

#### SUMMARY

Colonies of presumed hybrids of *Juniperus virginiana* L. with *J. horizontalis* Moench have been observed on the eastern fringe of the Driftless

Area in Wisconsin where the geographic ranges and ecological habitats of these species overlap. Characters occurring in a characteristically different combination in each of the species are found in random combinations in these colonies.

A comparative study of the somatic chromosome complements of the species and several of the presumed hybrids revealed an unbalance in those of the latter, evidenced by the presence of heterobrachial chromosomes without counterparts. The highest percentage of irregularities found at meiosis in pollen mother-cells of any plant of *J. virginiana* was 0.91% of *J. horizontalis* 1.91% and of their presumed hybrids 56.62%. Besides being more numerous than those of the putative parents, the irregularities of the presumed hybrids were of more diverse types, such as bridges, bridge-fragment configurations, laggards, micronuclei and different sized nuclei. The percentage of apparently normal pollen was found to range from 88.5 to 100% in *J. virginiana*, from 95.0 to 100% in *J. horizontalis*, and from 46.0 to 100% in the presumed hybrids.

This cytological evidence considerably strengthens the case for the occurrence of natural hybridization between *J. virginiana* and *J. horizontalis* first proposed by Fassett on standard taxonomic grounds.

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## ON THE EMBRYOLOGY OF SWERTIA CAROLINENSIS

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The gentian family is widely distributed throughout both the old and new worlds and, as pointed out by Rendle (1925), its representatives include dry sand-loving species, marsh or floating water-plants, grass-land plants, and many alpine forms. In external characteristics, however, marked differences exist between the terrestrial and marsh forms and many authors now place the latter in a new family, the Menyanthaceae.

Stolt (1921), in reviewing the literature and in his studies of *Erythraea*, *Gentiana*, *Exacum*, *Chlora*, *Halenia*, *Menyanthes*, *Villarsia* and *Limnanthemum*, has shown that the two families differ as much cytologically as they do externally. In the Menyanthaceae, he observed that the embryo sac was rather small and elongated, an integumental tapetum was present, the antipodals were regularly three in number and degenerated early, and a cellular endosperm was formed. The Gentianaceae, on the other hand, was characterized by a rounded or oblong embryo sac, the absence of an integumental tapetum, three or more variously developed antipodals, and a free nuclear endosperm.

These observations did not embrace the genus *Swertia*, however, which forms a conspicuous part of our flora, and since very little work on the Gentianaceae has been done in this country, *Swertia carolinensis* (Walt.) Baill. was selected and studied in the light of the above findings. An abundance of material has made possible a study which has not only confirmed Stolt's observations, in part, but has also revealed certain facts not previously reported.

*Swertia carolinensis* exhibits several peculiarities, such as the presence of squamulae intravaginales, a growth period of six or seven years before blooming, a flowering shaft of seven or eight feet, and a distinctly succulent nature. The plant occurs commonly throughout the eastern portion of the United States where it is remarkably local in its distribution. Its tall and beautiful dichasial cymes of sympetalous flowers are quite attractive and, except for the two-carpellate gynoeceium, are four-merous.

**Material and Methods.** Entire flower clusters, each containing several buds in different stages of development, were collected from early May to the end of the growing season. After removing the outer bracts, these clusters were split longitudinally and placed in the killing solution in the field. Upon returning to the laboratory the air was removed immediately by means of a suction pump.

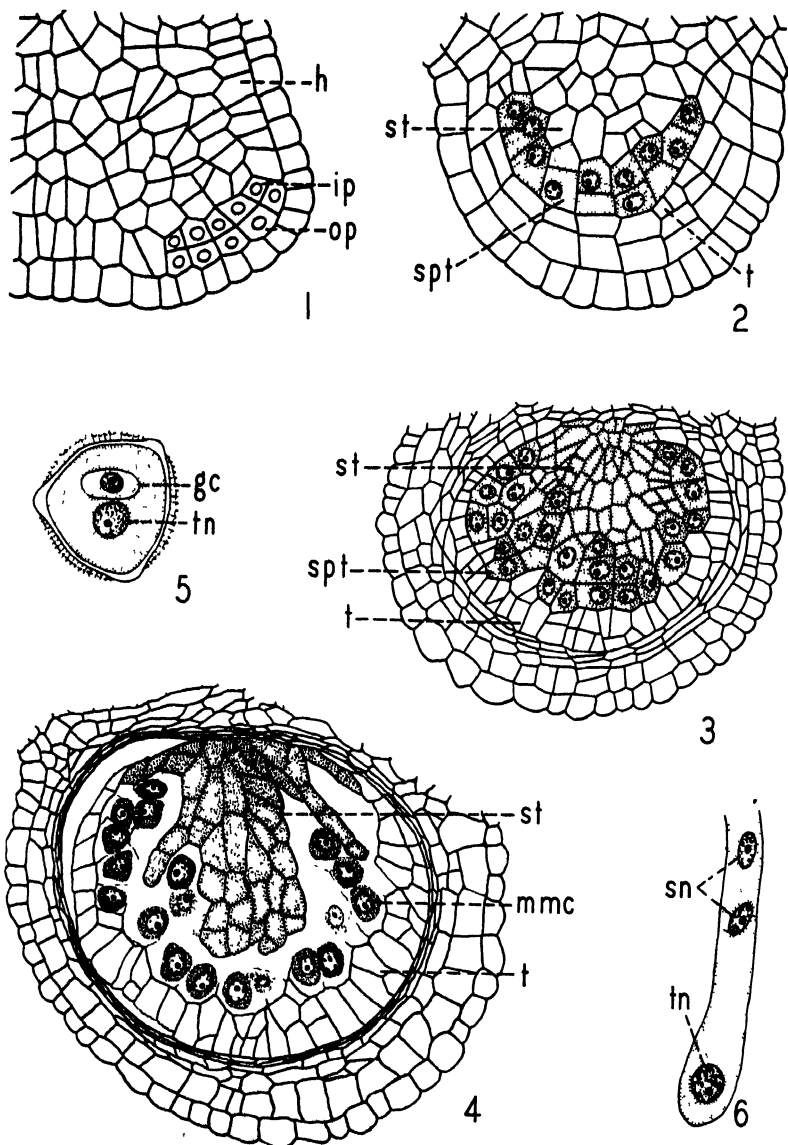
A variety of fixatives were employed, the most satisfactory results being obtained with formalin-acetic acid-alcohol and with Schaffner's weak chromo-acetic acid solution. The buds were imbedded in paraffin in the usual manner and transverse and longitudinal serial sections were cut from 8 to 15  $\mu$  in thickness. Flemming's triple and Foster's tannic acid-ferric chloride stains were generally employed. All cellular drawings were made with the aid of a camera lucida.

**Observations.** In the anther, four microsporangia are developed in the usual manner. A few hypodermal cells in each of the prominences of the young anther divide periclinally to produce inner and outer parietal layers (fig. 1). The inner parietals give rise to a variable number of primordial pollen mother cells which are easily recognized by their polygonal shape, larger nuclei, and dense, granular cytoplasm (fig. 2). These cells extend in several irregular vertical rows in each theca and increase in number somewhat to form the microspore mother cells. The thin-walled mother cells are usually disposed in an arc in transverse section (figs. 3, 4), although this unity may be broken in places by the interspersed simple parenchyma-like cells.

The outer parietals are then newly divided parallel to the epidermis, and, of the two layers thus formed, the inner gives rise to a nutritive layer, and the outer, or subepidermal, to an ephemeral middle layer and an endothecium. As many as six cell layers have been observed in the wall of the anther, exclusive of the epidermis. The inner derivatives of the outer parietal give rise to the nutritive layer by anticlinal cell division (fig. 2). The cells of this layer are always uninucleated but may increase in number somewhat as shown by figures 3 and 4. They do not completely enclose the pollen mother cells and are always external to the arc formed by them. These nutritive cells are little differentiated and are very vacuolate during the early stages of microspore formation.

A peculiar sterile tissue may be noted very early in the interior of each antheridial compartment (figs. 2, 3). These parenchyma-like cells occasionally extend entirely across the theca and separate the arc of the microspore mother cells into smaller groups. This ground tissue may be noted in each of the four prominences when the hypodermal cells divide periclinally to form the inner and outer parietals (fig. 1). The primordial pollen mother cells are easily recognized by the time they are no more than two cells removed from the epidermis (fig. 1), are few in number, and, in giving rise to the microspore mother cells, never lose their identity. With subsequent growth and enlargement of the anther, the sporogenous cells form a rather large arc and partially enclose the invading ground tissue which has developed (figs. 3, 4).





FIGS. 1-6. FIG. 1. Transverse section of a portion of a young anther showing inner and outer parietals.  $\times 300$ . FIG. 2. Transverse section of developing microsporangium.  $\times 300$ . FIGS. 3-4. The same successively older.  $\times 195$ . FIG. 5. Pollen grain showing contents.  $\times 500$ . FIG. 6. Tip end of pollen tube showing sperm nuclei and tube nucleus six hours after pollination.  $\times 500$ . gc, generative cell; h, hypodermis; ip, inner parietal; mmc, microspore mother cell; op, outer parietal; sn, sperm nuclei; spt, sporogenous tissue; st, sterile tissue; t, tapetum; tn, tube nucleus.

As noted in figure 3, these "internal" sterile cells are very vacuolated, but in later stages they seem to possess much more cytoplasmic material (fig. 4). Their position and orientation, as shown in figures 3 and 4, suggest that they have been instrumental in conducting nutrient material supplied by the anther into the sporangial cavity. As shown in figure 4, they maintain contact with the inner surface of the theca even after the "external" tapetum has broken loose from the sporangia wall. The "external" tapetum absorbs the wall layers of the sporangium and transfers the dissolved nutrient material to the developing pollen grains. Both nutritive layers are then finally absorbed *in situ* by the young microspores.

Two loculi are produced in the anther by disintegration and absorption of the partition between adjacent sporangia. This process begins just beneath that part of the epidermis which is to give rise to the stomium, and proceeds toward the connective. The stomium is formed by a radial elongation of eight or ten epidermal cells on each side of four or five small cells which remain unchanged. The small epidermal cells form a line of weakness along which the versatile anther dehisces longitudinally.

The second mitotic divisions are simultaneous, as is characteristic for the dicotyledons, and a tetrahedral tetrad is produced. Cytokinesis is accomplished by means of the cell plate. The pollen grain is small and has three germ pores. The generative cell is oval, and its nucleus is small in comparison with the tube nucleus (fig. 5). In this condition the pollen grains are shed from the rigorously protandrous stamens.

The style terminates in two large stigmatic lobes which bend backward when receptive. Covering their upper surfaces are large, thin-walled, simple papillae. Immediately beneath the papillate cells, a number of small vascular strands may be observed in transverse section. These veins tend to anastomose as they near the base of the stigma and pass down through the solid style as two separate bundles, one to each carpel. Arriving at the ovarian wall they divide again and give rise to the well developed placental bundles. Each strand traverses the entire length of its corresponding placenta but never extends into the funiculus.

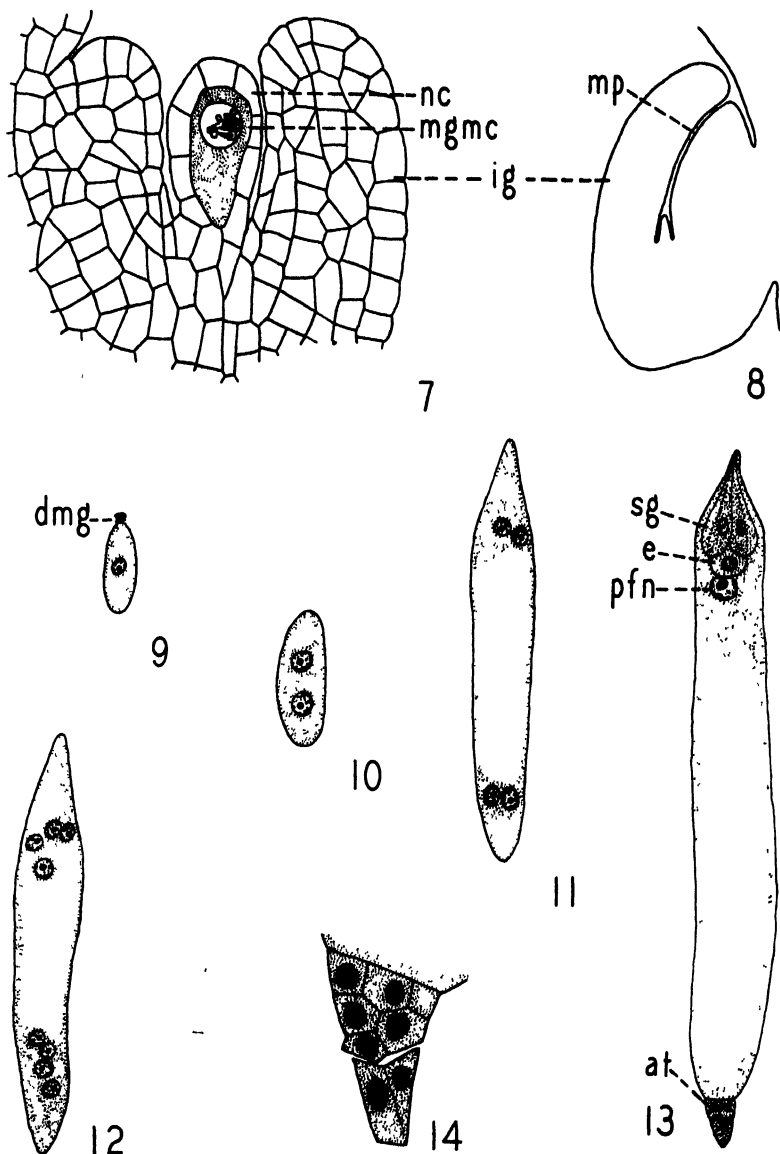
Pollen tubes, coming from monosiphonous pollen grains which germinate on the papillae covered stigmas, penetrate the elongated epidermal cells and soon enter the small vascular strands lying beneath them. Following these veins, the tubes are conducted to the placental bundles from which they emerge at different levels to enter the micropylar canals. Growing out at the surface of the placenta, the pollen tube advances to the nearby micropyle of the anatropous ovule and grows down through the canal to the egg apparatus. While the conduction of the pollen tube is thus endotrophic, for the most part, it becomes ectotrophic in passing over from

the placenta. The pollen tubes grow rather rapidly and usually reach the embryo sac within nine or ten hours after pollination. Figure 6 shows the end of a tube with the two small oval gametes already formed six hours after pollination.

The megagametophyte is of the monosporic *normal type*, involving five successive divisions of the megaspore mother cell before formation of the female gamete. The megaspore mother cell lies immediately beneath the epidermal layer of the nucellus in the central upper portion. It arises directly from a single primary archesporium and is easily distinguished from the other hypodermal cells by its larger size (fig. 7). A single integument is initiated near the base of the ovule at about the same time. This covering reaches the tip of the nucellus during the early prophase of the meiotic divisions (fig. 7) and, growing rapidly, soon extends much beyond its summit, adhering laterally along one side to the wall of the ovary, so that an anatropous ovule is formed. It consists finally of sixteen to eighteen cell layers, and forms a long curved micropyle which opens very close to the placenta (fig. 8).

In both the first and second meiotic divisions of the megaspore mother cell, the spindles lie in a longitudinal direction of the nucellus, and a linear tetrad of potential megaspores is produced. The chalazal spore becomes the functional megaspore while the remaining cells of the tetrad are absorbed. The megaspore, growing considerably, is soon characterized by a centrally located nucleus, surrounded by cytoplasm, and with a large vacuole in each end (fig. 9). Three successive nuclear divisions then ensue, and a normal seven-celled embryo sac is produced in the usual manner (figs. 10, 11, 12, 13). In so doing, the two polar nuclei move along the wall of the elongated megaspore, meet near the center, and fuse before the pollen tube empties its contents into the embryo sac. The large fusion nucleus with its enormous nucleolus then moves back near the egg cell (fig. 13). During the first phase of embryo sac formation, involving vacuolation and the first nuclear division of the megaspore, the epidermal cells of the nucellus covering the megaspore are crushed and absorbed, and the developing embryo sac comes to lie next to the integument.

A slight variation from the normal type of embryo sac formation is often exhibited by the chalazal half where development is somewhat more rapid than that in the micropylar end. The three antipodals may show signs of early disintegration (fig. 13), or there may be an increase in number by the time the embryo sac has matured, followed by disintegration and absorption (fig. 14). These cells are always uninucleated and distinct, but it was not determined whether the increase is due to mitosis or ami-



FIGS. 7-14. FIG. 7. Longitudinal section through portion of ovule showing megaspore mother cell.  $\times 365$ . FIG. 8. Longitudinal section through young ovule showing integuments and micropyle.  $\times 48$ . FIG. 9. The functional megaspore showing remains of disintegrating spores.  $\times 365$ . FIGS. 10-12. Stages in the development of the megagametophyte.  $\times 365$ . FIG. 13. Longitudinal section of mature embryo sac.  $\times 365$ . FIG. 14. Longitudinal section of chalazal end of embryo sac showing eight antipodals.  $\times 560$ . at, antipodals; dmg, degenerating megaspores; e, egg cell; ig, integument; mgmc, megaspore mother cell; mp, micropyle; nc, nucellus; pfn, polar fusion nucleus; sg, synergid.

tosis. The process takes place rapidly, and no mitotic figure was observed.

The pollen tube empties its contents, usually into one of the synergids, about ten hours after pollination. The receiving cell undergoes some change and immediately begins to disintegrate, as shown by its staining reactions to gentian violet, while the other synergid may remain quite unchanged for a time. As shown in figure 15, one sperm unites with the egg nucleus and the other with the fused polars. Starch grains, unloaded by the pollen tube into the embryo sac, have been omitted in this drawing. Upon being discharged into the embryo sac, the two gametes migrate very quickly to their destined places, and it has not been determined which one makes contact first. After fusion of the polar fusion nucleus with the secondary male nucleus, the primary endosperm nucleus thus formed remains quiescent while syngamy proceeds within the egg cell. The synergids and the contents of the pollen tube are usually absorbed before the first division of the endosperm nucleus.

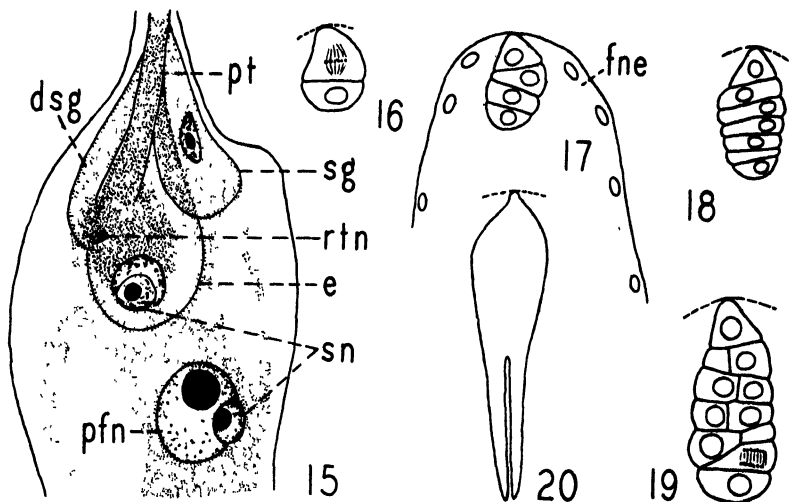
The first noticeable change in the embryo sac after fertilization occurs in the primary endosperm nucleus. It usually descends in the cytoplasm along the wall to near the middle of the embryo sac, where it undergoes division. Successive simultaneous divisions follow rather quickly, the free nuclei distributing themselves more or less evenly in the thin peripheral layer of cytoplasm (fig. 17). At a favorable moment, one may see them all at the same time showing the mitotic figure. During this period of hasty division the nuclei tend to be of fusiform shape, but become more or less globular as multiplication continues and the peripheral layer of cytoplasm increases in thickness. Cellulose membranes then appear rapidly between the peripheral nuclei and the process continues centripetally until the endosperm becomes an organized tissue of large, polygonal, parenchyma cells more or less isodiametric in shape. Wall formation is irregular, as shown by the open and closed boxes.

The fertilized egg remains unicellular for a long time, its first division being transverse and taking place after eight to sixteen endosperm nuclei have formed. As shown in figures 16, 17, and 18, transverse divisions continue until a simple row of seven or eight cells has been formed. When this stage is reached, longitudinal divisions set in, and a small cylindrical body, with blunt free end, is produced (fig. 19). This form is maintained during subsequent development until the cotyledons begin to appear.

The suspensor cells cannot be distinguished during the early stages of embryogeny, but, after the shaft-like body increases somewhat in diameter, seven or eight tiers of cells with four or more cells in each tier are recognized. With further growth, the embryo digests a small amount of the

surrounding endosperm in the micropylar region and finally assumes the form shown in figure 20, consisting of a small terete hypocotyl and two well formed cotyledons. The lower end of the hypocotyl is root and it possesses a small root cap.

Simultaneously with the development of the endosperm and embryo, the embryo sac, as well as the entire ovule, increases in size. The integument, which early manifests symptoms of absorption, is almost completely consumed during the later developmental stages of the ovule. Only the epidermal layer, which becomes the testa of the seed, survives the destruction. By means of continued anticlinal divisions in this layer, a wing two cells thick is formed around the edge of the smooth, flattened seed. The small, terete embryo is imbedded in the micropylar end of the copious endosperm in which food is stored chiefly in the form of protein.



FIGS. 15-20. FIG. 15. Longitudinal section through micropylar end of embryo sac showing double fertilization.  $\times 560$ . FIGS. 16-19. Early stages in the development of the embryo.  $\times 365$ . FIG. 20. Matured embryo showing cotyledons.  $\times 48$ . ds, disintegrating synergid; e, egg cell; fne, free nuclear endosperm; pfn, polar fusion nucleus; pt, pollen tube; rtn, remains of tube nucleus; sg, synergid; sn, sperm nuclei.

**Discussion.** As shown in the foregoing, the embryology of *Swertia carolinensis* is essentially like that described by Stolt (1921) for the Gentianaceae. A free nuclear endosperm and three or more weakly developed antipodals are formed. There is no integumental tapetum. A slight variation may be noted in the embryo sac, however, which perhaps more closely resembles the small elongated forms found in the Menyanthaceae.

Microsporogenesis was considered briefly by Stolt (1921) in only two

species. In *Swertia carolinensis*, however, the presence of sterile tissue in the microsporangia is of considerable interest. The occurrence of such tissue is not rare although it has generally been regarded as potentially sporogenous. Campbell (1898), for example, pointed out that in the pollen sacs of certain Naiadaceae some cells do not form pollen. An analogous situation was demonstrated by Bonnet (1911) in several species of the Onagraceae where the pollen sac is divided by partitions of sterile tissue. Guérin (1926) made a similar observation in several species of *Gentiana* and in *Swertia perennis*. In *Swertia carolinensis*, however, this "internal" mass of sterile cells, which functions as a tapetum, evidently does not arise from the inner parietal layer and consequently has no sporogenous potentialities. It is merely a natural "invasion" of the primary ground tissue of the anther into the microsporangial cavity. This phenomenon becomes evident if one follows rather carefully the earlier developmental stages of the theca (figs. 1, 2, 3).

Guérin (1926) states that these sterile cells finally take on the appearance of amoeboid tapetal cells in *Swertia perennis* but this phenomenon was not observed in *Swertia carolinensis*. The tapetal walls persist for some time, and there is no wandering of tapetal cells in between the maturing microspores, as described by Picket (1916) for *Arisaema*, or by Duggar (1900) for *Symplocarpus* and *Peltandra*.

The development of the megagametophyte differs in no essential way from that described for several species of the Gentianaceae. A variation of three or more weakly developed antipodals was also observed by Stolt (1921) in *Gentiana lutea*, *G. asclepiadea*, *G. nivalis*, *G. cruciata*, *G. tibetica*, *G. walujewi*, and *G. straminea*. Greatly enlarged antipodals, which evidently play an important physiological role in the development of the embryo sac, were found in *Swertia longifolia*, a closely related species, by Jacobson-Paley (1920).

The single integument observed in *Swertia carolinensis* is characteristic of the Gentianaceae. And as observed by Guérin (1903) in *Halenia elliptica* and *Gentiana campestris*, it becomes more strongly developed in the micropylar part than at the sides of the nucellus. All but the epidermis is absorbed as the ovule further develops.

Double fertilization was observed although it was not determined which sperm makes contact first. Jacobson-Paley (1920), however, noted that fertilization of either the chalazal polar nucleus or of the fused polars always preceded that of the egg in *Swertia longifolia*.

In the division of the primary endosperm nucleus, the spindle occupies various positions with reference to the long axis of the embryo sac and a free nuclear endosperm, followed by cell wall formation, is developed.

This, and the very small embryo, as pointed out by Schnarf (1931), are both typical for the Gentianaceae.

#### SUMMARY

1. The embryology of *Swertia carolinensis*, a gentian, is described and compared with that of other species and genera in the family.

2. A nutritive tissue of peculiar origin, apparently sterile, invades the microsporangial cavity and aids the regular tapetum during the development of the microspores.

3. The megagametophyte is of the monosporic *normal type*, involving five successive divisions of the megaspore mother cell before formation of the female gamete. It is much elongated at maturity and often consists of more than three weakly developed antipodals.

4. An integumentary tapetum is not formed although all but the epidermis of the single integument is absorbed during ovule development.

5. Entrance of the pollen tube is porogamous. Double fertilization occurs, and the primary endosperm nucleus so formed remains quiescent while syngamy proceeds within the egg cell.

6. The formation of a free nuclear endosperm always precedes that of embryo development.

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## LIGULE-ENDODERMIS OF ISOETES MURICATA VAR. BRAUNII

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Casparian strips and the endodermal like layer at the ligule base of *Isoetes macrospora* Dur. have been described (Dunlop 1949). This finding was of enough interest to cause the writer to investigate and compare the ligule-endodermis of *I. macrospora* with that of another species of *Isoetes* found in Wisconsin.

**Material and Methods.** Axes of *Isoetes muricata* var. *Braunii* (Dur.) Reed, were collected in Washburn county in about four feet of water from Bass Lake, T-38-N, R-11-W, and killed in Belling's modification of Navashin's fixative. Sections were stained with the crystal-violet-iodine-picric-acid counterstain technique with uniformly good results.

**Discussion and Observations.** Longitudinal sections of the stem region of *I. muricata* var. *Braunii* showing the development of a series of leaves illustrate the rather rapid early growth of the ligule, (fig. 1A), and show that the ligule-endodermis is differentiated very early in leaf development and represents part of the leaf proper; however, Casparian strips cannot be demonstrated until some time later in leaf development.

The base of each older ligule is ensheathed by a mature endodermis and as in *I. macrospora* each cell of this specialized layer possesses a complete Casparian strip in the four radial walls, (fig. 1B). The Casparian strips are bright blue when stained with crystal-violet and their path about the radial walls is remarkably distinct (fig. 2A). Stained with Sudan IV, the cross sections of the Casparian strips are faintly pink. They are anisotropic when rotated between crossed prisms, this being observed best in lightly stained or unstained preparations.

Vascular tissue associated with the ligule is similar to that in *I. macrospora* both in position and amount. While tracheids do not completely enclose the ligule-endodermis there is a considerable supply distributed throughout the region of the endodermis, and in the plane of the leaf trace this vascular supply reaches all the way around the ligule base from the velum region to the top of the ligule base. In frontal sections of the ligule base the ensheathing distribution of tracheids is probably best seen (fig. 2B). Reticulate tracheids seem to be absent from the vascular sheath of the endodermis although they are found in the trace near by.

Casparian strips of the two Wisconsin species are approximately the same width, ca.  $2\mu$ ; however, the two species differ in cell size, nuclear volume, and chromosome number as well as in the sculpture of their meg-

aspore surface. The volume of the endodermal cells of *I. macrospora* is approximately 51 per cent greater than the volume of endodermal cells of *I. muricata* var. *Braunii*. The volume of nuclei of the endodermal layer of *I. macrospora* is approximately  $144.0 \mu^3$  while those of *I. muricata* var. *Braunii* are approximately  $73.2 \mu^3$ . This nuclear volume ratio of 2:1 is consistent in the writer's preparations. The diploid chromosome number of *I. muricata* var. *Braunii* is 24-26 and that of *I. macrospora* has been estimated at approximately twice as many (Dunlop 1949).

#### SUMMARY

1. Casparian strips are present in cells of a specialized layer of the leaf at the ligule base of *Isoetes muricata* var. *Braunii*.
2. The name ligule-endodermis is suggested for this specialized tissue.
3. A considerable supply of tracheids are present at the ligule base and are very closely associated with the endodermis, many of them being in contact with the walls of the endodermal cells.
4. The ligule-endodermis of *I. muricata* var. *Braunii* and *I. macrospora* are alike in structure but differ in nuclear and cell size.
5. The presence of a ligule-endodermis in two species of *Isoetes* indicate the probability of its occurrence in other species of the genus.
6. The location of the ligule-endodermis, its high degree of development, and its association with vascular tissue seem to indicate that it is related functionally to the ligule.

The writer wishes to thank Dr. Eugene S. McDonough and Dr. William N. Steil for critical reading of the note and examination of the preparations.

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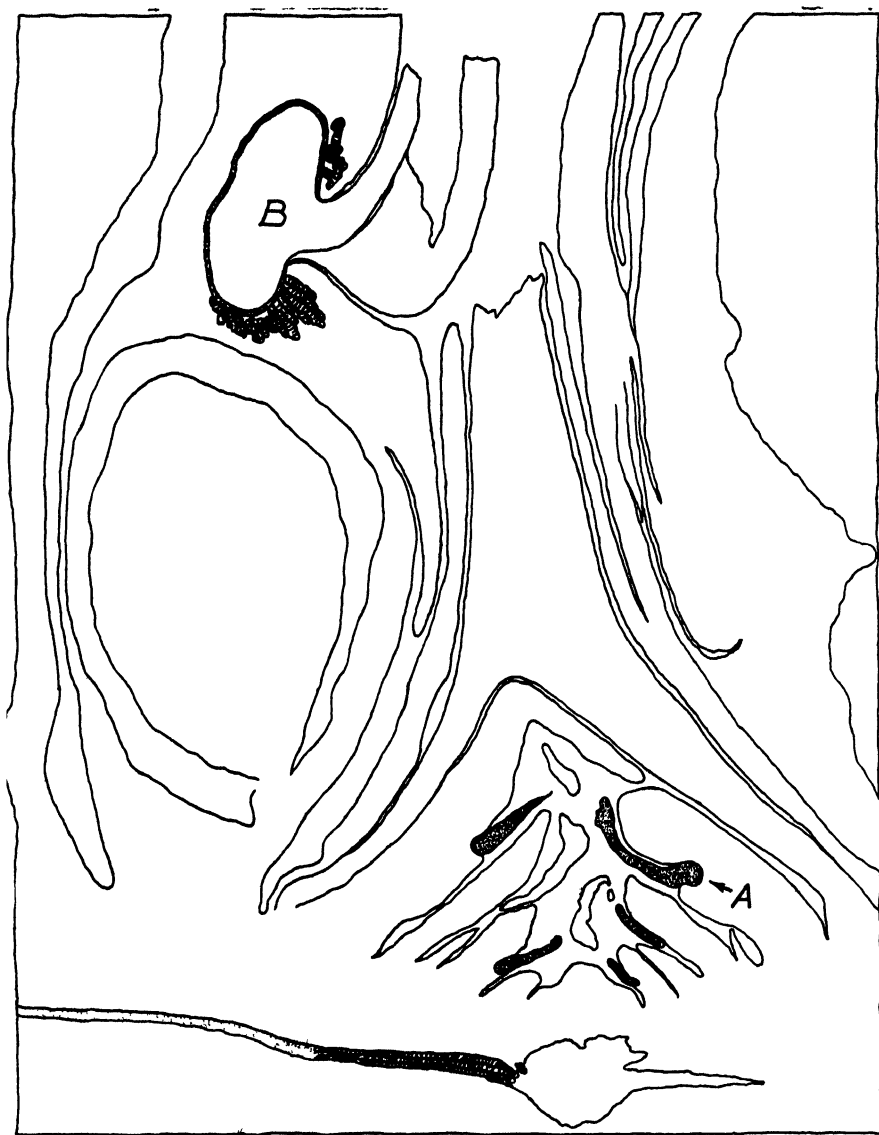


FIG. 1. Longitudinal section of stem tip region of *I. muricata* var. *Brauni*. A. Early development of ligule. B. Older ligule with ligule endodermis and vascular supply.

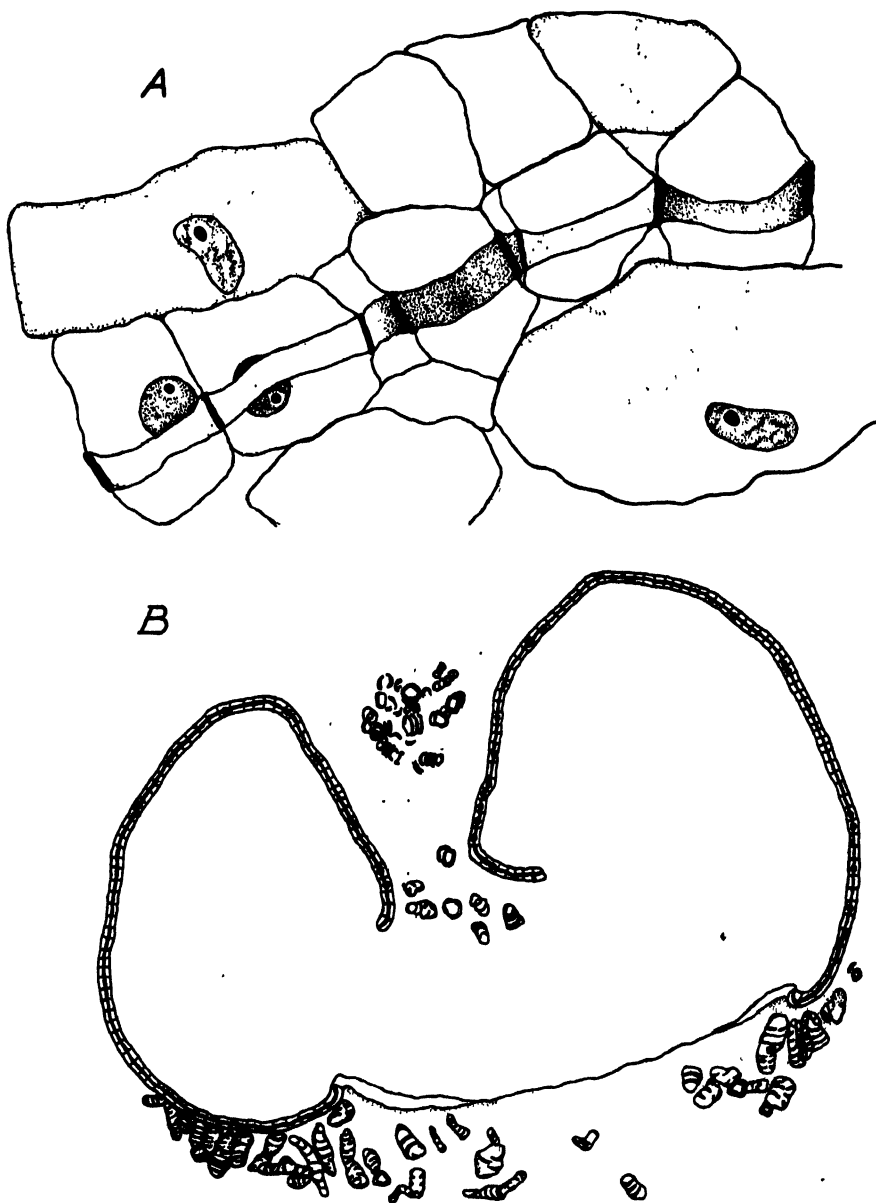


FIG. 2. Ligule-endodermis of *I. muricata* var. *Braunii*. A. Casparian strips in endodermal cells. B. Frontal section of ligule base showing tracheid distribution.

A REINTERPRETATION OF SCHIZOSTEGE LIDGATEI  
(BAKER) HILLEBRAND<sup>1</sup>

WARREN H. WAGNER, JR.

The genus *Schizostege* Hillebrand (1888) was erected on the anomalous endemic Hawaiian fern, *Cheilanthes Lidgatei* Baker (1883). Hillebrand referred to the type species as, "A fern of the habit and size of *Pteris biaurita*, more akin to *Pteris* than *Cheilanthes*. In fact, it might be considered as a *Pteris* with interrupted sori and involucre. . . ." Less than a decade later, Christ (1897) placed it in *Pteris*, an interpretation maintained by Diels (1899) and Christensen (1906).

In 1906 Copeland revived the genus *Schizostege* and added to it two new species from the Philippines; these were described as more like *Cheilanthes* in general appearance. With Copeland's publication the distinctness of the genus was recognized anew and Christ (1910) called the Hawaiian plant a striking intermediate between *Pteris* and *Cheilanthes*, resembling the former in leaf-form, and the latter in sori. In 1913, Christensen likewise took up the genus as comprising three species and had by 1934, included it as genus Number 125 under the Polypodiaceae (in the older sense), following Number 123, *Pteris* with 269 species, and Number 124, *Hemipteris*, a monotypic genus of New Guinea. An extreme view of the affinities of this genus was expressed by Winifred J. Robinson (1912), that, "The habit of *Schizostege* closely resembles that of *Pteris* but the relation is no closer than that of *Cheilanthes* to *Pteris* or of *Pellaea* to *Cheilanthes*."

The scarcity of the three species included in *Schizostege* has added to the difficulty in evaluating the generic group. Although the Hawaiian one has been placed at different times and by different authors at various points on or near a morphological line connecting *Pteris* and *Cheilanthes*, an alternative hypothesis—that of mutation—has been suggested to explain its peculiarities. Christensen (1925) stated, "I am inclined to believe that the obscure plant called *Schizostege Lydgatei* Hill. . . is a mutant, derivate from a species of *Pteris* (*P. excelsa* Gaud.?)." Copeland (1941) recently wrote that "The status of *Schizostege* is . . . dubious. An enormous number of ferns have been collected in Hawaii in the past fifty years but *Schizostege* has never reappeared. It may have been a monstrous *Pteris*, unable to reproduce itself."

<sup>1</sup> *Lidgatei* was the original spelling of the specific name, but the later authors adopted *Lydgatei*. As his publication on Hawaiian ferns (Lidgate, 1873) also bears this spelling of his name, it is assumed he changed it at some later time, so the first spelling is accepted here.

In the summer of 1947, the writer was able to make a search for *Schizosteg* in the course of an attempt to study this and other ferns which seemingly had disappeared from the Hawaiian flora. To Dr. E. B. Copeland I owe the original instruction and encouragement to make the expedition, and to Dr. Harold St. John, Miss Marie C. Neal, and Mr. Eugene Horner, as well as many others, I am thankful for much aid. The following discussion is an effort to describe the occurrence of *Schizosteg* *Lidgatei*, to extend the description of the sporophyte, and to evaluate the evidence concerning its distinctness as a species and the generic problem involved.

**Occurrence:** As the type locality for this rare plant Baker (l.c.) gave only the island of Oahu, and Hillebrand noted only the two localities at which he had found it. Only two additional localities have been listed subsequently, and these with no details except for Robinson's vague description, "on ground." (l.c.). Because the plant's rarity has had an important bearing on its interpretation, the following, rather detailed notes should be recorded.

On July 18, 1947, the writer explored part of Waihee Gulch in West Maui where this species was first discovered by Hillebrand "in a sterile state at a waterfall near the head of the gulch" but was unable to find any of the plants. This gulch is very steep, with ferns in abundance on the damp bottoms of the slopes. There are several side-gulches along the upper Waihee River, any one of which might have been Hillebrand's original locality. Forbes' specimens from Molokai were found on the bank of a stream on the slopes of Olokui above Waiehu ("Elev. 3000 ft.?" ) in September 1912, an area which I have not revisited. The stations on either of these two islands have thus not to my knowledge been rediscovered.

Of the three known general localities on Oahu, all in the Koolau Range, I am not aware that it has been recollected in the valley of Wailupe where it was found in a fertile state for the first time by Hillebrand's son and Lidgate. However, several collectors, including Professor A. B. Lyons, one-time science teacher at Punahou, found it during the period 1865-1890 in a valley which has its head at the base of the summit peak of Konahuanui, back of Honolulu. This valley connects with Nuuanu near the head of Pauoa. The plants, a dozen or more, were confined to a limited area on a steep bank immediately above the stream bed, not far from the head of the valley. The stream bed was dry except during rainy weather. (Eugene Horner: letters of July 15 and October 18, 1948, and February 7, 1949.) Mr. Horner visited this station, reported here for the first time, several times in the years 1896-97, and found fertile fronds on each visit. He has kindly permitted me to study this material.

No further collections on Oahu are known until May, 1909, when Forbes, the first botanist of the B. P. Bishop Museum, in the company of the late

C. Montague Cooke, found two plants in the Koolau Mountains between Punuluu and Kaipapau (without numbers on the specimens seen). An additional collection labeled simply "Waiahole Pali, with A. F. Judd, C. M. Cooke, and Porter, Feb. 6, 1912, No. 1746 O[ahu]" was made subsequently. With directions provided by Mr. Cooke, the writer, with Messrs. Charles and Robert St. John, and R. Toupin, made a search on August 31, 1947 for the Punuluu locality, which Mr. Cooke stated was about twenty yards to the left of the continuation of the Castle Trail along the second stream beyond the ridge. As it turned out, this one was not reached, but the first stream, Koluanui Stream, was explored and three large plants were found at the sharp bend about one-half mile downstream from the point at which the trail crosses the stream. At this spot Koluanui Stream is approximately 1750 feet in altitude. The situation in which the plants were growing is a rocky hillside of about 70° slope, and they grew about fifteen feet above the stream, in rich dark humus, pH 4.5 with a LaMotte "Soil Teskit." The three plants were shaded when the sun was overhead, and the *Metrosideros* trees on the mossy slope are abundantly clothed with mosses, indicating rain-forest humidity and rainfall (fig. 1). The fronds are borne erect by the stiff and robust stipes (fig. 3), but the blades, with fullest laminar area exposed to light, are oriented downward parallel to the slope, which is shaded from above. One of these plants was taken for later study. This general area harbors feral pigs which are known to denude hillsides and frequently to root out whole fern-plants. Other ferns growing near-by were *Sphenomeris chusana* (L.) Copel., *Lastrea globulifera* Brack., *Cibotium Chamissoi* Kaulf., *Elaphoglossum reticulatum* (Kaulf.) Gaud., *Dicranopteris linearis* (Burm.) Underw., and *Cyclosorus cyatheoides* (Kaulf.) Farwell. *Sadleria squarrosa* (Gaud.) Maxon, another wet-forest plant, is frequent in the general area.

The difficulty of recognizing this fern in the field should make the following remarks of use to field-botanists. The appearance of this plant was likened by Baker to *Woodwardia radicans*, but Hillebrand compared it to *Pteris biaurita*. As shown in figure 2, the indentation of the veins in the shiny, crisp, living lamina, and the dentations of the fertile margins in these plants with interrupted sori when seen from above, lessen the resemblance of the plant in nature to *P. biaurita* or its local relative, *P. excelsa*. While the latter comparison is doubtless closer phylogenetically, it may not be as helpful as comparison with local ferns less closely related. From a distance young *Cibotium* plants might be confused, but the endemic Hawaiian *Ctenitis honolulensis* (Hook.) Copel. seemed to resemble it much more closely when viewed from a distance of ten or more feet. In general habit and in the dark gray-green color, the appearance is quite similar. Seen closer, however, the *Ctenitis* has various differences which distinguish it.

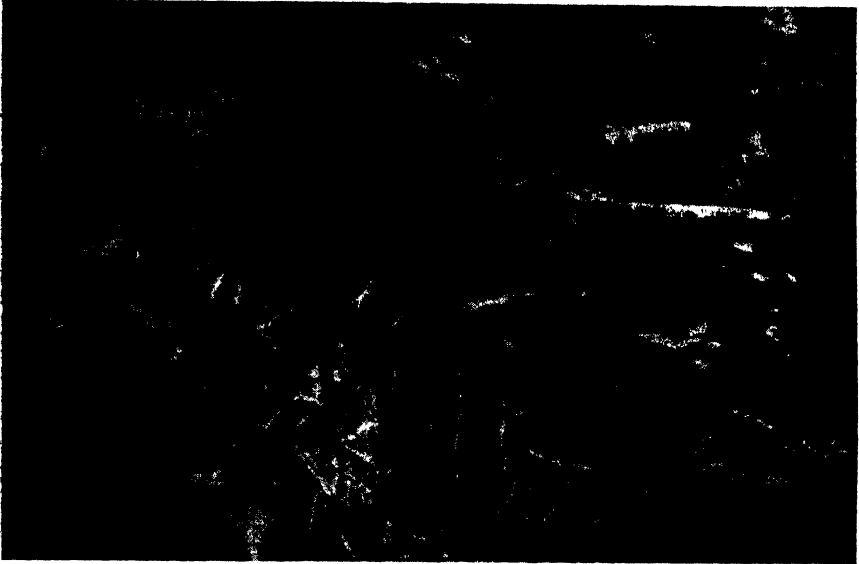


FIG. 1. Habitat of *Pteris Lidgatei*. Plant in center of picture directly under overhanging moss-covered roots. Koluanui Stream, Koolau Mountains, Oahu, T. H. May 23, 1948. (Robert P. St. John).

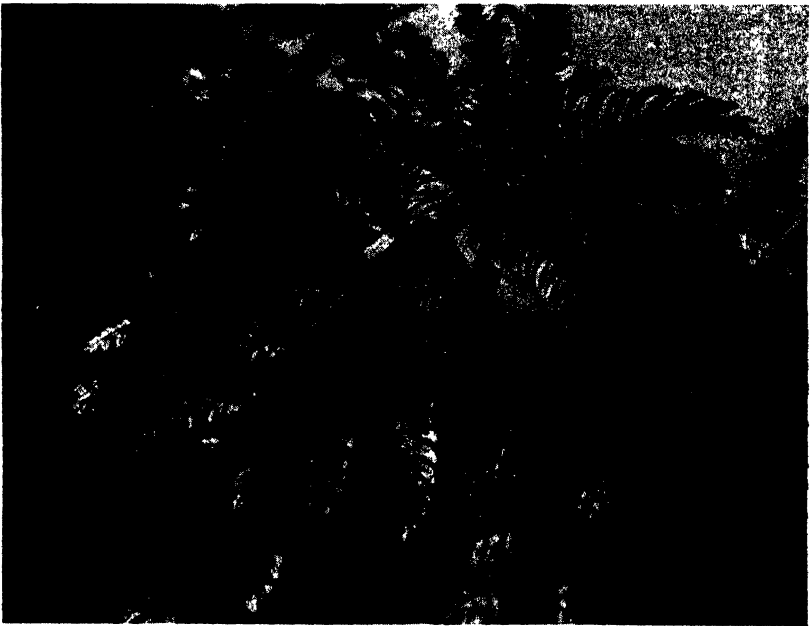


FIG. 2. Living frond of *Pteris Lidgatei* with separate sori, showing depression of vein and costules, and shiny, coriaceous lamina.  $\frac{1}{2}$   $\times$  natural size. (University of Hawaii).



In the present plant the young living fronds are pale gray-green. The heavily cutinized leaf-surfaces become roughened by depression of the costules and veins. The texture of the living mature pinnæ is remarkably thick, and they are brittle. The lobes are broken readily when roughly handled in collecting and pressing. The stout stipes and rachises are dark gray-brown and highly polished. However, the stipes and the long, shiny chestnut-brown scales which invest their bases are hidden by the tangled vegetation of the habitat. Only the flat frond faces can be seen.

All references to this plant indicate its scarcity: Robinson noted an interval of about twenty-five years between Hillebrand's and Forbes' collec-



FIG. 3. Living plant of *Pteris Lidgatei* showing frond habit and thick stipes. 1/10  $\times$  natural size. (University of Hawaii).

tions on Oahu, but these were apparently the only ones known to her. Copeland recently (1947) raised the suspicion that it might no longer exist in nature. As the collection described here followed the previous one by 35 years, reasons for the paucity of collections might be asked. An infrequency of occurrence combined with a tendency to grow among numerous mosses and ferns, and its similarity to other, more common genera in casual aspect are probably the factors which make this Hawaiian fern so poorly represented in herbaria. In all likelihood, these factors rather than a chance ori-

gin of the plant by mutation, explain this condition. It is my belief that deliberate search for it on other islands, especially Kauai, would reveal other localities. It should be sought at altitudes between 1000 and 3000 feet, on steep, wooded, fern-covered slopes in wet forest, growing in rich, acid humus above the beds of streams. It is urged, however, that plant collectors observe caution so this endemic fern will be perpetuated; its scarcity, like that of certain other Hawaiian plants, emphasizes that the living, self-reproducing plant in natural occurrences may be many times more useful to future students than abundant packets of parched herbarium mummies.

**Description of the sporophyte:** Coarse herb, 0.5–1.0 meters tall (fig. 3). Rhizome horizontal, 1.5 cm. thick, 10.0 cm. or more long when mature, solenostelic, the pith 0.5 cm. in diameter, the cortex 0.5 cm. across radially, drying gray-brown (not cream-white as in *Pteris excelsa*). Rhizome bearing about eight green fronds and one or two browned, dead fronds (August), and several remaining stipe bases, the stipes originating very close around the rhizome. Roots extremely numerous, matted, nearly 1 mm. in diameter, 3–15 cm. long, and tapering but little; root-branchlets 0.5 mm. in diameter, borne at intervals of about 1 cm.; the whole root system invested densely with dark red-brown, delicate, straight hairs, 2 mm. long. Stipe bases and rhizome apex clothed with crowded, glabrous, shiny, atrocastaneous paleae, 0.8–1.5 cm. long, 0.1–1.5 mm. broad, linear, gradually narrowing to the attenuate tips of only several cells width. Scale cells elongate, 5–10 times as long as broad, with square or oblique end-walls, the walls dark brown translucent except in the thin-walled cells of similar shape along the margins in one or more layers. Scales remaining several centimeters along stipe but soon falling above this area, leaving remote, tiny black, wart-like spots, 0.5–2.0 mm. in diameter. Fronds, including the stipes, 80 (60–95) cm. long and 40 (20–45) cm. broad, the blades spreading, not dimorphic and usually all fertile. Stipe 45 (25–50) cm. long, 3–6 mm. in diameter, gray-brown, except for lowest several centimeters where it is dark red-brown. Stipe vascular tissue omega-shaped in cross section (as in *Pteris excelsa*). Blade oblong-deltoid to broadly ovate-deltoid, the lamina coriaceous, brittle, dark gray-green (pale gray-green when newly unfolded, and often blotched dark-brown in age). Stomata on lower surface, parallel, the long axes of the openings parallel to the veinlets but avoiding them in an epidermal strip about four times the veinlet width; the pair of guard-cells located distally on more oval and less undulate-walled epidermal cells. Hairs similar to *Eupteris* species on undersurface, remote, with 3 (2) oblong cells, the basal one longest, the apical one with rounded apex and usually tannin-filled. Hairs most frequent in the angles between the costae and costules. Blade bipinnate at base, the basal pinnae provided with 1–4 long basal auricles, the upper pinnae lacking these. Terminal pinna like the lateral pinnae in form, but larger (15–25 cm.), and relatively larger in more immature fronds. All pinnae deeply lobed, becoming less deeply lobed near the apices and in some individuals (as in fig. 6). Rachis not winged with lamina, brownish straw-colored, shiny, sulcate. Lateral pinna-pairs six or less (“8–10” Hillebrand), sub-opposite, only the basal pair in mature fronds definitely stalked, the stalk

3-4 mm. long, the remaining pinnae usually sessile. Angle of pinnae  $70^{\circ}$  ( $60^{\circ}$ - $80^{\circ}$ ). Unlobed pinna-tips 3-5 cm. long, broad-caudate. Lowest pinnae 14-27 cm. long, with auricles 12 (2-19) cm. long. Medial pinna-pairs 17 (11-21) cm. long, 5 (4.0-5.5) cm. broad in the middle. Sterile margins of lobes dentate with sinuses up to 0.5 mm. in depth, or occasionally nearly entire, mostly with two veinlet termini per tooth, but at tip only one undivided vein terminus per tooth. Vein plan of lobes pinnate, free (except for

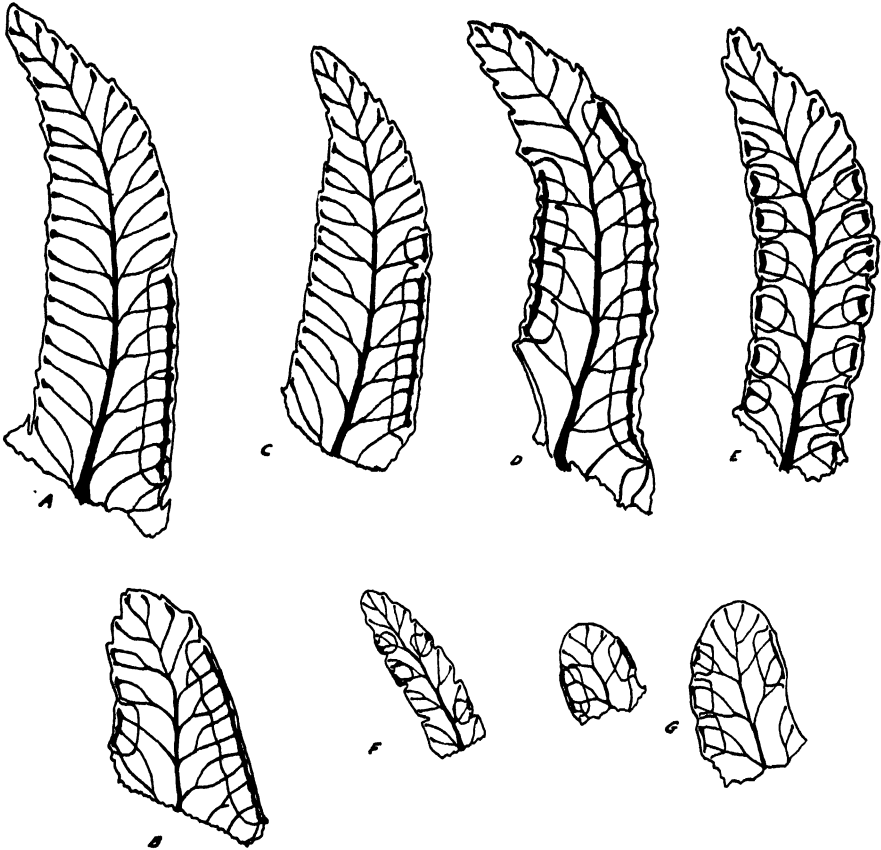


FIG. 4. A-E, *Pteris Lidgatei*. A. *Horner s.n.*, complete coenosorus. B. *Forbes 556Mo.*, complete coenosori. C. *Horner s.n.*, apical interruption of coenosorus. D. *Horner s.n.*, lobulation of indusium. E. *Wagner 5762*, typical discrete sori. F. *Schizostege calocarpa*, *Copeland 1707*, structure of teeth and sori. G. *Schizostege pachysora*, *Copeland 1715*, two segments showing the entire margins and sori, and variable anastomoses.

occasional terminal anastomoses as in fig. 4, a). Central lobes with 11 (10-12) mostly once-forked pairs of veins originating along costule; distal lobes with only 2-3 vein-pairs; proximal lobes with 5-18 vein-pairs. Lobes falcate, 10 (9-13) mm. broad, mostly oblong or oblong-triangular, ascending at tips, broadly pointed to nearly obtuse, cut to within 4-1 mm. of the

costa. Lowest vein-pairs along costules of the largest lobes often forked twice, the first furcation next to the costule. Veins and veinlets sunken, and shallowly corrugating the upper laminar surface. Veinlets, including all elongate cells, 120–130 microns in breadth in the middle.

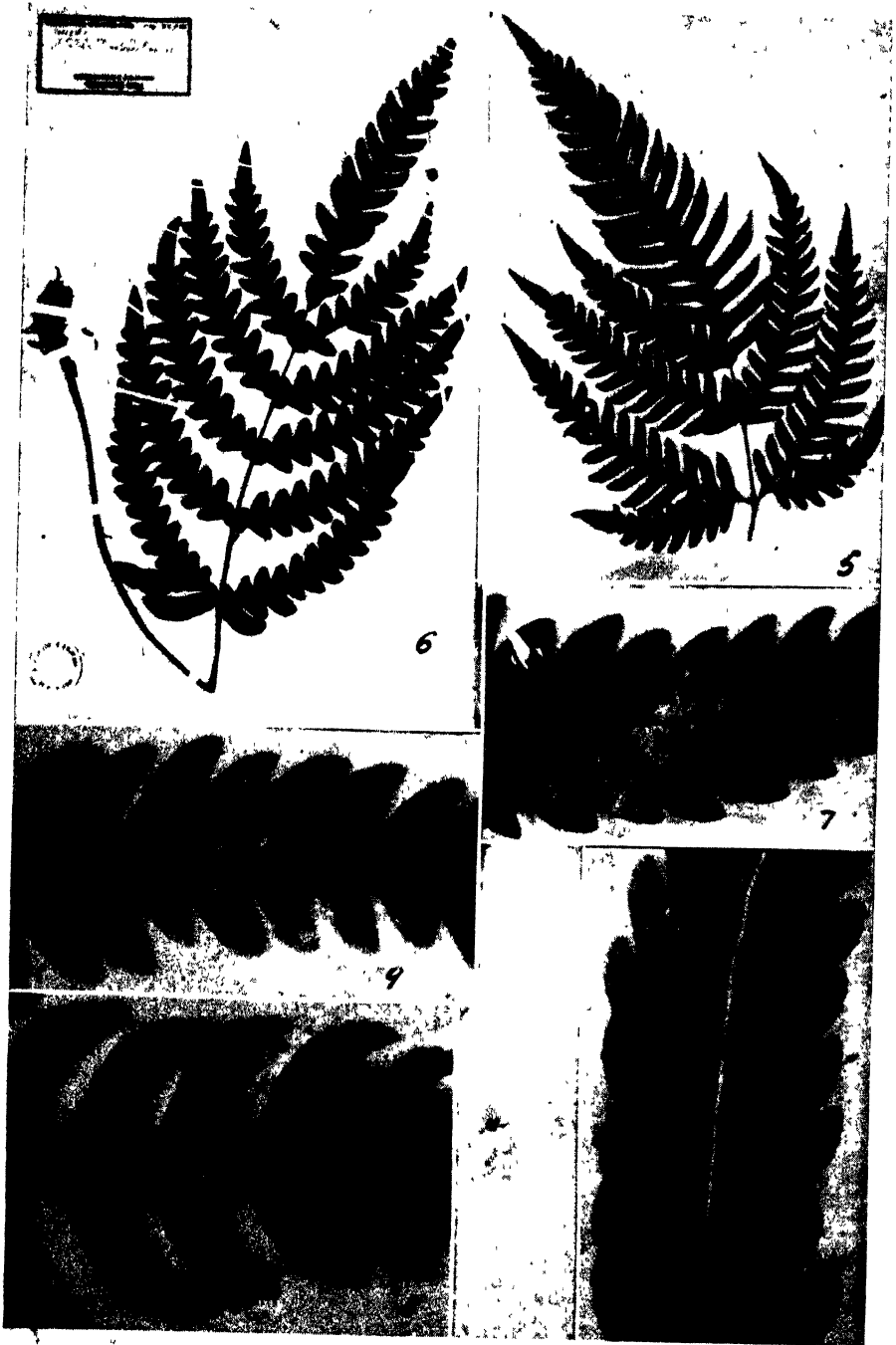
Sori apparently marginal in position, either continuously fused in coenosori (fig. 4, a and b) or more typically separated into distinct sori (fig. 4, e), intermediate conditions being also common (fig. 4, c and d). Coenosori 4.31 mm. in length, often separated at distal ends (fig. 4, c); separate sori 1.5–2.5 mm. long. Indusium of thick texture, dull white except in age when it becomes irregularly or evenly blackish tannin-stained (fig. 8), a broad, entire flap, a more or less lobed flap, or separated into rounded triangular or square discrete indusia, 1.5–2.5 mm. long, 1.5–2.0 mm. broad. Receptacle likewise continuous to regularly separated into equal divisions, subtended correspondingly by a continuous connecting cross-vein between the upcurved termini of the lateral veinlets, or by separated cross-veinlets between sister veinlet tips; cross-vein near tip often reduced to T-shaped expansions of simple lateral veinlets. Fertile cross-vein 325–375 microns in width except at junctures with lateral veinlets where it expands to 400 or more microns. Fertile cross-vein tracheids mostly oblong or ovoid with spiral or spiral-reticulate secondary wall, 50–150 or more microns long, 5–35 microns broad. Sporangia crowded, numerous, large; stalk of two cell layers, 3–5 cells tall. Sides of capsule with about fifteen more or less quadrangular thin-walled cells, the walls nearly straight. Annulus with 21 (17–22) thickened cells; stomium with three thick-walled cells, and four thin-walled cells below these, and two or three above. Stomial side of sporangium less convex than opposite side, sometimes nearly straight. Capsule 500–560 microns tall, 415–530 microns broad. Spore numbers counted in herbarium material 51–55, probably 64 when all formed and present. Spores tetrahedral, averaging 57–81 microns, trilete, rarely bilateral, triangular in polar view, sculpture irregular, rather crowded with warts of various sizes, tetrad scar distinct, bordered by ridges, and occasionally not reaching the angles (Selling, 1946, p. 51, figs. 111–118; Brown 1931, fig. 15f).

**Material examined:** *Forbes s.n.* Koolauloa Mts. between Punahuu and Kaipaupau, Oahu, May 8–13, 1909 (NY, BM); July 8, 1909 (US); Punahou Mts., Oahu, May, 1909 (NY). These are probably all from the same locality. All specimens show separate sori.

*Forbes 1746 O[ahu]*. Waiahole Pali, with A. F. Judd, C. M. Cooke, and Porter, February 6, 1912 (BM). Separate sori.

*Hillebrand and Lydgate s.n.* *Schizopteris Lydgatei* Hbr., *Cheilanthes Baker*, Flora Hawaiiensis, collected by Dr. William Hillebrand and J. M. Lydgate, Ex Herbarium J. M. Lydgate (BM); *Schizopteris Lydgatei*, Oahu, Hillebrand, The New York Botanical Garden, Herbarium of Lucien M. Underwood (NY). These fragments are probably from Wailupe, Oahu.

*Horner s.n.* Base of the summit peak of Konahuanui, Koolau Range, Oahu, 1896–97 (Horner Herbarium and UC). These comprise two apical pinnae, one frond tip with apical pinna, and three lateral pinnae, two middle fragments, two herbarium sheets including the specimen illustrated in figure 5, and a blade or blade apex with a large terminal pinna and one pair of laterals. All specimens are coenosoral with a tendency to separate sori.



*Wagner 5762*. Koluanui Stream, Hauula Forest Reserve, Koolau Range, Oahu, August 31, 1947 (UC). Specimens all with distinct sori.

*Forbes 556 Mo[loka'i]*. Slopes of Olokui, above Waiehu, elev. 3000 ft.† September, 1912 (BM). A young frond with rhizome, coenosoral (fig. 6).

**Additional illustrations:** Baker, 1886, Pl. 1635, figs. 1-4: figures 1 and 2 illustrate an irregular tendency for coalescence of sori in a pinna, and a pinnule intermediate between those with coenosori and those with entirely separate sori. Figures 3 and 4 illustrate the sorus. Christ, 1910, fig. 106: A whole young frond, apparently with fusion of sori, and the apex of another, showing discrete sori. Robinson, 1912, Pl. 41: An apical portion of a frond with three pairs of lateral pinnae and discrete sori, and a large basal pinna with two auricles is illustrated.

**Relationships:** As shown in the foregoing description and figures, some of the materials of the plant currently called *Schizostegia Lidgatei* lack completely the characteristic interruption of sori, the original basis for generic separation. Of the few localities known, specimens from two—Konahuanui, Oahu, and Olokui, Molokai—have typical pteroid coenosori. While all the specimens seen from the more northerly localities in the Koolau Range have entirely separate sori, those of Hillebrand's from Wailupe Valley, Oahu, show occasional tendencies toward coenosoral fusion. The Maui plants found by Hillebrand were sterile. In view of the collections with coenosori, and the various conformities of this plant with known elements in *Pteris* to be discussed below, the proposal is made that it be reinterpreted as *Pteris Lidgatei* (Baker) Christ, and that name will be used here.

Pointing out that difficulty in distinguishing and evaluating species is characteristic of the Hawaiian flora, Copeland (1947) remarked that "*Schizostegia* is dubious as a single species." Christensen, more than a score of years earlier, had speculated that this plant might be a mutant of *Pteris excelsa*. Yet, having seen living plants of both of these entities in their native habitats and having examined them comparatively in the herbarium, I cannot endorse the latter suggestions. On the contrary, *P. excelsa* differs from its supposed offshoot not only in lacking the marked tendency for regular soral division—a "schizostegoid tendency"—but also by its occurrence in different habitats, its narrower fronds, basal pinnae which have but one auricle or none, the usually much thinner laminar texture and paler color,

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FIGS. 5-10. FIG. 5. Frond with coenosori, Konahuanui, Oahu, T. H. Eugene Horner (Horner Herbarium)  $\frac{1}{2} \times$  natural size. FIG. 6. Young frond with coenosori and unusually blunt lobes, Olokui, Molokai, T. H., C. B. Forbes 556 Mo. (B. P. Bishop Museum)  $\frac{1}{2} \times$  natural size. FIG. 7. Pinna with coenosori, Horner s.n. (University of California) natural size. FIG. 8. Pinna tip with coenosori and undulate indusia, showing tendency for black tannin accumulation in old indusia, Horner s.n. (University of California) Natural size. FIG. 9. Pinna with deeply lobed indusia, Horner s.n. (University of California) Natural size. FIG. 10. Pinna with typical separate sori, Wagner 5762 (University of California) Natural size.

narrower and longer segments, finer serration of the margins, more compound and closer venation, narrower and more fragile indusium, smaller and differing spores and sporangia, and various other features. That *P. Lidgatei* is a mutant in the conventional genetical sense, of *P. excelsa* is obviously doubtful; that so many apparently unrelated characters would mutate simultaneously seems very unlikely. The constant differences of *P. Lidgatei* from any other known fern would appear to make its specific status unquestionable.

Although the plant under consideration was first described in *Cheilanthes*, and Copeland (1906) regarded the Philippine ferns he placed with it as approaching *Cheilanthes*, a sound concept of immediate affinity between *Schizostege* or *Pteris* and *Cheilanthes* has not been developed by any author. On the other hand, Bower (1928) regarded *Pteris* as a derivative from dicksonioid ferns with marginal, bi-indusiate sori, and *Cheilanthes* as probably descended from schizaeaceous ancestors, never more than uni-indusiate from the beginning. He stated that, "To us who now realize that a very similar soral structure may arise along distinct phyletic lines, the habit characters acquire additional value in these comparisons." Remarking that the habit of *Hypolepis* is different from the group of *Cheilanthes*, he considered *Dennstaedtia* and *Hypolepis*, themselves with indusiate ancestors, as likely prototypes for both the davallioid and pteroid ferns. Exindusiate osmundaceous and schizaeaceous types were his supposed ancestors of his gymnogrammoid forms, including *Cheilanthes*, through ferns in which the uni-indusiate condition had arisen by the "phyletic slide" of marginal sporangia and subsequent modification of the leaf-tissue of the margin as an indusium.

This viewpoint of the origin of *Cheilanthes* is not shared by most authors, and Christensen (1938) related his "Gymnogrammeoideae" to the "Pteridoideae." Copeland (1947) revived the possibility that *Cheilanthes* (including *Notholaena*) may be derived from or related to *Hypolepis*, noting a species of the latter genus similar to *Cheilanthes* in habit. He states that *Cheilanthes* has conspicuous characters in common with the "Pteridoideae." Neither of these hypotheses, it should be noted, places *Pteris* and *Cheilanthes* in direct line with each other in evolution. Although the immediate relationship of the Hawaiian *Schizostege* can be deduced with a fair degree of assurance, this cannot be said for the Philippine plants. Their morphology must be studied comparatively, however, before valid grounds can be established for interpreting them as possible phylogenetic links between pteroid and cheilanthoid ferns.

The Hawaiian fern appears actually to be an isolated insular derivative of the group of *Pteris quadriaurita* Retzius, which evolved perhaps in an ancient Hawaiian flora and is comparable to such unique local species of

large genera as *Microsorium spectrum* (Kaulf.) Copel. and *Athyrium Macraei* (H. & G.) Copel. The group of *P. quadriaurita* in the strict sense comprises many species, some of which are very similar. Hieronymus (1914), restricts this pantropic group to all species of *Eupteris* with pinnate leaf-blades, more or less deeply divided lateral pinnae, and of which the lowest pair or pairs bear one to three (very rarely more) basal auricles. In all of them there is a terminal pinna similar to but mostly larger than the upper lateral pinnae. The venation is free and the lateral veins of the lobes are mostly forked, only several of the apical ones being simple. The lowest lateral veins almost always end above the sinuses between the lobes. This definition of Hieronymus is perhaps too strict; other obviously closely related elements, such as *P. biaurita* L., with veinlets anastomosing along the costae, and probably even more different forms should be included if this is to represent a natural section of the genus. Hillebrand's comparison of *P. Lidgatei* to *P. biaurita* referred to the habit of the plant, but in the type of venation the present plant agrees with *P. quadriaurita*. The veinlets are thicker and more remote than usual. The hairs of this fern agree in form with those of other allegedly glabrous *Eupteris* species. Although surely distinct from it, the nearest fern in Hawaii to *P. Lidgatei* is *P. excelsa*, which Hillebrand (1888) called, "The largest species of the quadriaurita group." These *Pteris* species, as well as the *Litobrochia* section and other groups, bear small spines or elongate pointed flaps at the costule bases on the wings of the costae. As such appendages appear to be absent in the section *Lonchitis* and the groups of *Pteris cretica* and *P. longifolia*, this character is of importance in assessing affinities within the genus, as had been shown as early as 1839, in the enumeration of *Pteris* species by Agardh. The differences of the Philippine plants in all of these characters will be discussed below.

The unique division of the submarginal line of sporangia into separate groups to form individual "involucres" each with its own receptacle, fertile cross-vein, and indusial flap has been the one and only real distinction of the Hawaiian *Schizostegia* from *Pteris*. The schizostegoid condition of separate sori, however, should not be considered primitive to the pteroid coenosorus. Bower's placement of such types as *Paesia*, *Pteridium*, and *Histiopteris*—all with coenosori—as hypothetical analogues of ancestors of *Pteris*, supports this conclusion. The schizostegoid sorus is more probably a modification of the usual *Pteris* sorus.

Even if there were not coenosoral specimens, the fact that *Schizostegia* was originally distinguished by its regularly broken line of sori does not mean that this distinction in itself is necessarily of valid generic value. Diversity in this respect, but without generic division because of it, is seen in such pteridaceous genera as *Adiantum* and *Lindsaea*. The coenosoral con-



dition is found in such examples as *Adiantum lucidum* (Cav.) Sw. and *Lindsaea ensifolia* Sw., and discrete soral arrangements in *Adiantum obliquum* Willd. and *Lindsaea Macraeana* (H. & A.) Copel. Although such analogies have certain weaknesses, it should be noted again that the existence of strikingly parallel modifications in different fern families has led to the evaluation of soral structure, in numerous instances, as being of less and less critical significance in fern systematics. A convenient example of radically different sori in plants of close affinity is the modification seen in a single previously mentioned Hawaiian endemic, *Athyrium Macraei*. Here occur both typical dorsal athyrioid sori and sori terminal on vein extensions beyond the leaf-margins. Individuals with the latter type were formerly referred to an artificial genus, *Deparia*, in which were placed two unrelated elements, similar only in the sori. Apparently a similar state of affairs obtains in the genus *Schizostege*.

In *Pteris*, some species of the section *Lonchitis* (upheld by some authors as generically distinct) regularly show abbreviated sori located in the sinuses and separated by the sterile, distal lobe-margins. Mr. C. A. Weatherby (in a letter) called to my attention the fact that the "West African *Pteris pteridioides* (Hook.) Ballard (*P. brevisora* Baker) has such short sori that Hooker originally described it as a *Hypolepis*." It is interesting also to note that Christ (1897) placed this plant closest to the Hawaiian one. *Pteris* species of other sections show a tendency toward interruption of coenosori as indicated by Sprau (1933). The same tendency may be seen readily in young or incompletely fertile examples of *P. excelsa* in Hawaii (e.g. *Wagner 5251*, Haleakala, Maui). Thus the abbreviation or interruption of coenosori is not unusual in *Pteris*.

The breakage of coenosori observed regularly in fully mature *P. Lidgatei* appears to depend on characters of the margins. Diels' use (l.c.) of the serrate or toothed margin of the sterile segments as a character for distinguishing this plant from the *P. quadriaurita* group does not cover the situation. Various species of the group possess toothed sterile margins, these almost always with fine, one-nerved teeth, at least near the apices of the segments. Diels' other criteria, segment and pinna pointing and complexity of the blades, likewise do not hold. The teeth of sterile margins of *P. Lidgatei* serve not so much to separate it from other *Pteris* species as to explain the schizostegeoid sorus, which seems to depend on the spatial relationship of the bottoms of the sinuses to the line of sporangia. Such a conclusion differs from that of Hillebrand, who considered "the interruption not occasioned by a lobulation of the segment" (op. cit. p. 632), where he was presumably thinking of pinna margins of the *Lonchitis* type. The present interpretation stresses the form of the margins, the formation of indentations being reflected in the development of separate sori.

Toothed sterile margins in *Pteris* generally show from one veinlet-terminus to a tooth (dentate, with one veinlet per tooth) to two veinlet-termini to a tooth. In the latter condition the proximal veinlet is reflected by a marginal bulge or small point, the distal one serving a more conspicuous, longer point (essentially bidentate), or the proximal one shows no marginal bulge (dentate or crenate, with two veinlet-termini per tooth). In sterile margins of *P. Lidgatei* most of the teeth away from the segment tips belong to the latter category, and the two sterile veinlet branch-endings are nearly on a line with, or beyond, the sinuses. Since, as it is generally agreed, the pteroid indusium is "false," i.e., results from continued outgrowth of the margin beyond superficial sporangial initials (Bower, 1928), the schizostegeoid indusia appear to be homologues of these teeth. The two veinlet-termini present are evidently joined in the typical pteroid manner by the characteristic mass of specialized short tracheids subtending the receptacle. When indusia of herbarium specimens are dissected away from the thick, reflexed tissue of the leaf-margin, the folded-over margin in coenosoral specimens appears as a continuous band of tissue; but in specimens with discrete sori there remain instead tooth-like inward projections of the margins separated by sinuses, which correspond in position with those of the distal sterile margin. If this assumption is correct, an ontogenetic study might be expected to show that in development the line of sporangial initials is nearly congruent with, or beyond, an imaginary line connecting the sinuses of the developing leaf where the schizostegeoid sorus type is formed; the sporangial line would consequently be interrupted by the sinuses. Further growth could therefore result only in scalloped, infolded indusial segments, these in some cases overlapping laterally. As the size of teeth and dissection of coenosori do not appear to be correlated, the various soral conditions must be due to differences in the time of appearance of sporangial initials and sinuses. This and the related problem of factors connected with the origin of sporangial initials and its bearing on formation of commissural tracheid masses and indusia could be especially well studied in the present species because of the large size of the structures involved, and the presence of both separate sori and coenosori in the same species.<sup>3</sup> The distal portions of the lobes have simpler veins and deeper teeth. It is here that coenosoral fronds

<sup>3</sup> Parallel division of coenosori by toothed margins, dentate with two veinlets per tooth (in this case usually somewhat closer to bidentate), in which the larger sinuses are in line with sori is to be seen in a specimen of *P. dentata* Forsk., U.C. 398432. Here sporangial production is pronounced in the lower halves of the segment margins, and in these lower parts typical coenosori are found. But acropetally there is a transition to the sterile and toothed condition of the margin by breaking up of the coenosorus, and individual sori here are schizostegeoid, served by two veinlets and separated by acute sinuses. *P. tremula* R. Br. specimens, e.g. U.S. 61265, U.C. 61264, and U.C. 42965, show a similar condition.

most often show occasional discrete sori (fig. 4, c). On strongly soriferous plants the sori extend relatively closer to the tips. These, like the distal teeth of sterile lobes, are served by only one veinlet, modified terminally by the "T-shaped" type of receptacular vein described by Hillebrand.

The type of segment described here showing pteroid coenosori with continuous fertile veins subtending the uninterrupted receptacles would be expected to form sporangial initials prior to marginal sinuses in ontogeny, so that such sinuses fail to appear and the indusium then develops as an entire flap. Intermediate development is seen in those examples where the indusium is continuous at the base, but lobed along its free margin, as in some of the sori on the fragments illustrated by Baker (1886) and some of Horner's specimens (fig. 4, d). Hillebrand, with the material available to him, had not seen complete junction take place in the intra-marginal veinlet even when several sori coalesced. This imperfectly connected condition of the fertile vein may likewise be considered intermediate between typical schizostegeoid plants and the material described here. It may be that only fully mature leaves express the marginal condition believed responsible for complete coenosoral separation. Forbes' Molokai specimen, the small frond illustrated by Christ (1910), and the Horner material are evidently all more or less juvenile and possess more or less uninterrupted coenosori. Further field study or, even better, observation of cultivated plants grown from spores, is needed.

In addition to the inclination toward regular coenosoral interruption, this species is notable for the exceedingly thick texture of the lamina and indusium, especially in old dark-blotched fronds. Such a texture is, however, not unknown in *Pteris*, as is shown by the Andean *P. coriacea* Desv. (e.g. *U. C.* 679440). Individual specimens of other species in the quadriaurita group, which more closely resemble the present plant, also show similarly thick and rigid textures, e.g. *P. arguta* Ait. (*U. C.* 205101 and *U. C.* 203282), and a specimen of *P. excelsa* from Kwantung, China (*U. C.* 611422). Among other Hawaiian "pteridophytes" also, there are conspicuous tendencies in certain genera toward coriaceousness. Thus the two local species of *Psilotum*, the two native *Ophioglossum* species, and the one *Vittaria*, contrast with their nearest relatives to the south and west in thickness of branch or frond. The texture of *P. Lidgatei*, then, is not unique in the genus, and is paralleled by textures in certain other Hawaiian plants (perhaps evolved by similar selective factors?). Although it is not as large in overall dimensions as many species of *Pteris*, the thickness of lamina, large spores and sporangia, stout stipes, heavy veins broadly spaced, large scales, and wide, tough indusia bespeak its general robustness.

The two other ferns placed in *Schizostege* were collected in April, 1905,

along a creek at San Ramon, District of Zamboanga, Mindanao, Philippine Islands, by Copeland. *Schizostegia pachysora* was found at about 2500 feet altitude, and *S. calocarpa*, with the more divided fronds, was found further upstream at about 3000 feet. Neither has been recollected in this locality nor found elsewhere. Of them, Copeland (1947) recently wrote, "Whether they are really congeneric with that of Hawaii or merely fit the fairly detailed generic diagnosis remains questionable."

The most obvious differences between the Hawaiian species and the two Philippine ones are vegetative. Unlike the type species, the frond structure in both of the other plants (cf. Copeland 1906, Pl. 12; Christ 1910, fig. 107) is clearly different from the quadriaurita group of *Pteris*, as Copeland has already indicated (1947), and cannot be matched in other sections of that genus. But close similarities between the two Philippine plants themselves show that they are congeneric, and share various features precluding obvious relationship to *P. Lidgatei*. The smaller fronds (40-65 cm. tall) of the Philippine plants are conspicuously narrower in outline, and the apex is formed by gradual reduction in symmetry, rather than by a single, marked, apical pinna. The rachises are scaly and dull and so strongly winged that only about one to three of the narrow pinna-pairs in the simpler species and six to nine in the more dissected are really free. The rest of the pinnae merge into the wings. Neither has segment margins like *P. Lidgatei*, as will be discussed further. The spine-like free or appressed appendages along the ventral surfaces of the costae at the segment bases, found in many *Pteris* species including *P. Lidgatei*, are absent in the Philippine plants. Vein anastomoses in the lamina in *Schizostegia pachysora* contrast sharply with the Hawaiian plant, but *S. calocarpa* possesses mostly free veins, probably consequent upon greater dissection. Both of the latter species have a fleshy and thicker texture when alive but when dry are papyraceous, instead of brittle-coriaceous, and are much more hairy, especially on the axes, than *Pteris Lidgatei*.

Resemblance between the sori of the Philippine and Hawaiian plants seems at first sight considerable, but a careful comparison with excellent materials of the latter, which were unavailable when the Philippine plants were first described, shows that this is probably coincidental. Such a mode of coenosoral separation as suggested for *P. Lidgatei* cannot be seen here because *Schizostegia pachysora* has margins which are perfectly entire, and *S. calocarpa* has much broader teeth of a different form than those of the Hawaiian plant. Discrete sori in the last are served regularly by two veinlet termini (apically by one), while in *S. pachysora* there is variation from one to five veinlets terminating in an individual sorus, and in *S. calocarpa* the sori are served mostly by only one veinlet-terminus. The very broad

serrations of *S. calocarpa* show from one to four veinlet-termini, but only one (occasionally two) ends in a sorus (fig. 4,f). There may thus be half or more of the tooth margin sterile, and as the sorus in these cases is proximal on the tooth, it is the distal pointed portion of the tooth which is free. Consequently, in these ferns the "schizostegoid" condition must have come about by some different course.

In the absence of manifest affinities to known elements in *Pteris*, it is possible that *Schizostegia pachysora* and *S. calocarpa* may together merit separation from that genus. It would be desirable, however, to await more collections and further study before erecting a new genus. Christ seems to have come to consider the Hawaiian plant as separate from *Pteris* only after he had seen the two Philippine plants with apparently identical sori. It is evident, however, that these similarities in sori are only superficial. It may be concluded, then, that a genus defined by this doubtful character and embracing two elements with widely different fronds—only one of these with known close prototypes in *Pteris*—is artificial.

#### SUMMARY

The genus *Schizostegia* Hillebrand was based on *Cheilanthes Lidgatei* Baker, an anomalous Hawaiian fern originally considered to differ from *Pteris* in having interrupted sori. Two Philippine plants with apparently similar sori were placed with it. All three are rare and poorly known ferns, and the Hawaiian had been suggested to be a possible mutant of *Pteris excelsa* Gaud. A rediscovery of this plant in 1947 showed that it occurred on steep wooded slopes in wet forest, growing in acid humus above a stream. An examination of hitherto unstudied material indicates that it should be reinterpreted as *Pteris Lidgatei* (Baker) Christ. Specimens from two of the six known localities possess uninterrupted pteroid coenosori with continuous fertile veinlets. The characteristics of the plant are so marked that it is undoubtedly a distinct species, but any close relationship with the genus *Cheilanthes* is questionable. In general features, especially frond habit, type of venation, and appendages of the costae, it conforms with the quadriaurita group of *Pteris*. Since short sori are found in certain *Pteris* species as a mature state or as a transient juvenile form, and since such pteridaceous genera as *Adiantum* and *Lindsaea* contain species with coenosori and species with discrete sori, this by itself does not appear to be a natural generic criterion in this case. It is suggested that the separate sori found in typical *P. Lidgatei* may be due to the formation of the margins of the lobes, involving a growth correlation between the establishment of the sinuses of the teeth and the development of the sporangial initials. The thick leaf-texture is not unique in *Pteris*. The two Philippine plants, mutually

closely related, placed with the Hawaiian plant, differ from it and the *P. quadriaurita* group in the habit of the frond with the terminal pinna formed by gradual reduction in symmetry and the winged rachis, the segment margins, indument, absence of costal appendages, venation, and texture. Soral similarities are probably due to convergent evolution and do not provide evidence of affinity. A genus comprising these two dissimilar elements is therefore considered artificial.

DEPARTMENT OF BOTANY

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## TORREYA

## PROCEEDINGS OF THE CLUB

**Minutes of the Meeting of May 3, 1949.** The meeting was opened at 8:05 P.M. by President Matzke at Columbia University; 30 members and friends were present. The minutes of the preceding meeting were read and approved.

Dr. Berthe Delaporte of the Institut Pasteur, Paris, presented a paper on "The Structure of Bacteria." Her abstract follows:

A great many observations have been published about the structure of Bacteria, without any one receiving general acceptance. Recently, however, there has been such close agreement among the observations of different studies using new methods of staining—either after acid hydrolysis (Feulgen, Giemsa) or after enzymatic digestion—that it now seems probable that we are arriving at a knowledge of the true structure of bacterial cells in many species.

Only the simultaneous use of many different methods of observation (on living cells without staining; with vital staining; with staining of metachromatic corpuscles, lipids, glycogen, and nuclear substance) can enable us to form a concept of the structure of bacterial cells.

The cells of most bacterial species have metachromatic corpuscles and lipid globules; in addition to these, certain species also have some glycogen, and others (sulfur bacteria) have sulfur globules. In every bacterial cell there is also a nuclear element, containing—as do the cell nuclei of every plant and animal species—deoxyribonucleic acid. This element divides at the moment of cellular division, before the formation of the transverse membrane, and has many characteristics of a nucleus. Nevertheless, its intimate structure is not sufficiently well known to permit us, at present, to identify it as a true nucleus.

The shape of the nuclear element depends on the shape of the cell. It is a spherical mass in cocci, a central ovoid mass in ovoid cells, a roundish granule in very short rods, and an elongated body, situated lengthwise of the cell, in long rods (axial thread). When reserve substances (lipids, glycogen, metachromatic, sulfur, etc.) are found in the central part of the cell, they push against the nuclear element and deform it, and can also fragment it into several parts.

Division of the nuclear element takes place by simple stretching and separation into two identical parts, without any special internal structure being apparent. A granule lengthens, takes on a dumbbell shape, and then divides into two granules, which pull away from each other. An axial thread separates in the middle into two parts. A small rod, transverse to the long axis of the cell, divides lengthwise into two parts, which move away from each other in the direction of the long axis of the cell.

When a new culture is made, the cells soon enter a stage of very active multiplication, during which the nuclear elements divide more rapidly than the transverse membranes are formed. This results in cells that have two or four nuclear elements, sometimes more. In rods, each of the potential cells, consisting of one nuclear element with its surrounding cytoplasm, is usually

very short and approximately square; the nuclear element in these cells takes the form either of a compact mass or of a short transverse rod compressed between the adjacent substances. When the rhythm of divisions slows down, the cells have time to elongate between nuclear divisions and the nuclear element gradually resumes the shape typical of the species.

The spore of *Bacillus* species develops, in the beginning, from a fragment of nuclear substance, which surrounds itself with a homogeneous cytoplasm. This prespore grows slowly to the size of a normal spore, becoming ovoid in shape, with a nuclear element in the form of a short rod. This nuclear element migrates to the periphery of the sporal cytoplasm, often taking (for example, in *B. cereus*) a ring shape, most commonly seen in side view as a curved rod with slightly thickened extremities. In the course of this change the sporal cytoplasm alters its staining affinities and the spore becomes enclosed in a refractive membrane. During spore formation there is a progressive—not always total—disappearance of the nuclear substance and protoplasm that were in the sporangium, outside the spore. The spore is then liberated.

At germination, the spore swells while the nuclear element comes into the center, enlarges, undergoes various transformations, and then divides. At about this time the young rod emerges from the spore. Often two or three divisions of the nuclear element are completed before the first transverse membrane is visible. When the resting spore remains inside the remnant of the sporangium membrane, it is sometimes possible to see that at germination one or two granules of chromatic substances are discarded on the exterior surface of the spore coat; these granules are probably remnants of the nuclear substance of the sporangium, outside the spore.

After discussion the meeting adjourned at 9: 05.

**Minutes of the Meeting of May 17, 1949.** The meeting was opened at Hunter College, with President Matzke in the chair, at 8: 25 P.M.; 25 members and friends were present. The minutes of the preceding meeting were read and approved.

The following names were presented for membership in the Club: Sustaining Member: Kent H. McKnight, Provo, Utah; Active Members: Margery S. Anthony, Ann Arbor, Michigan; Earlene Atchison, Chapel Hill, North Carolina; Ernest Ball, Raleigh, North Carolina; John L. Blum, Buffalo, N. Y.; Paul R. Desjardins, Berkeley, California; James G. Dickson, Madison, Wisconsin; Beatrice B. Exner, Baton Rouge, Louisiana; A. Alfred Foster, Farmingdale, N. Y.; Luis E. Gregory, Turrialba, Costa Rica; H. J. E. Hardh, Tikkurila, Finland; Gunnar W. Harling, Stockholm, Sweden; Benedict A. Hall, Cortland, N. Y.; J. R. Holbert, Bloomington, Ind.; Thomas D. Howe, Defiance, Ohio; Beatrice Krauss, Honolulu, Hawaii; Lucien Levesque, Montreal, Canada; Karl Maramorosch, Brooklyn, N. Y.; Margaretha G. Mes, Pretoria, South Africa; John H. Mulahy, Mobile, Alabama; C. L. Porter, Laramie, Wyoming; Howard C. Reynolds, New York, N. Y.; Bruno Schusnig, Igls, Austria; Nils E. Svedelius, Uppsala, Sweden; Ida Werner, New York, N. Y.; Hugh Wilcox, Corvallis, Oregon; John J. Wurdack, New York, N. Y.; Justin Zender, Lawrenceburg, Indiana; Joseph G. Zoril, Fort Collins, Colorado; Associate Members: Nellie Allen, Manasquam, New Jersey; Hope Mathewson, New York, N. Y.; Jane Meyer, Yonkers, N. Y.; Mrs. R. E. Noble, Brooklyn, N. Y.; Henri Prat, Montreal, Canada; A. H. Sparrow, Upton, N. Y.; Prof. Van Itersen, Baarn, Netherlands; Clara Weigle, Trenton, N. J. All were elected.

Dr. Harold W. Rickett of the New York Botanical Garden addressed the Club on



"Travels of John Bradbury up the Missouri River in 1801 and 1811." His abstract follows:

John Bradbury (1768-1823) is known chiefly for certain specimens collected on the Missouri River in 1811, which served as the basis of new species described by Pursh in his *Flora*. These specimens are in the Academy of Natural Sciences of Philadelphia. Most of Bradbury's extant specimens, however, are preserved in the Public Museum of Liverpool, from which city Bradbury was sent out to America. These, with a packet of letters from or concerning Bradbury, it was the speaker's privilege to examine during the summer of 1948. Bradbury also published a book, *Travels in the Interior of America*, after his return to England in 1816. This contained a vivid account of the journey up the Missouri, of the vegetation and nature of the country, of various adventures with skunks, bears, and Indians; experiences which are confirmed and enlarged by some of the letters written from America. The letters also explain much that was hitherto unknown about the later history of the specimens, and explain how Pursh came by some of them. They also make clear just how Bradbury failed to realize the success which he anticipated; it was largely a matter of money, which both he and his sponsors had under-estimated. Impoverished by the expenses of his expedition, having lost many of the specimens gathered at such pains, Bradbury resigned from the service of the Liverpool Botanical Garden, and went to New York where he engaged (unsuccessfully) in business for several years. He returned to England only to find that Pursh had reaped the scientific reward of his collections; and finally returned to America with his family, first to St. Louis, later to Middletown, Kentucky, where he died only a few years later.

The meeting was adjourned at 9:25, and refreshments were served by members of the Hunter College botanical staff.

Respectfully submitted,

DONALD P. ROGERS,  
*Recording Secretary*

#### FIELD TRIP REPORTS

**May 1. Netcong, N. J.** Amid lowering skies and scattered showers, three carloads of dauntless souls gathered at the Netcong, N. J. railroad station Sunday morning May 1. Because of the fear that the heavens might open at any moment, the group adjourned to Maj. Barry's residences (several cottages and bungalows, including his new 4-story skyscraper designed to place the owner on a level with various species of bird life and afford a vista of woods and Budd Lake). Lunch was enjoyed in the rustic log cabin "Cotswold." Having decided that the rain might hold off a few hours, the group hiked up the Fire Tower for a view of rolling woodlands and too many nimbus clouds. Thence a brief trip to a blueberry swamp where we found the usual skunk cabbage, anemones, and other spring flowers, as well as a number of mosses. At this point the rain fell, Bill (ye hound dog) turned tail and streaked for a dry home, followed by most of the group, except for a few hardy souls who dug specimens amidst a warm spring downpour. An hour later the group was back at Cotswold in cozy chairs playing "Twenty Questions" 'till the rain should stop. The skies lightened somewhat and the three cars of flower lovers went by back roads to Waterloo. Enroute several stops were made to see cowslips (marsh marigolds), early ferns and a variety of other plants, as well as the shiny red leaves of young poison ivy. At Waterloo, the group inspected the ruins of the old Morris Canal locks of the vintage of 1800, and surveyed the inclined plane up which towboats filled with anthracite from Pennsylvania mines once journeyed to Jersey City. The hour

being late, the group adjourned to drive homewards, sorry that the weather had not permitted more time on flower study, but grateful that despite the showery day, there had been a chance to get together and enjoy some of the pleasures of seeing early flowers and opening green buds. Attendance: 10. Leader: Maj. Lyman F. Barry.

**May 1. Silver Lake, White Plains, N. Y.** A goodly number of plants were observed but nothing out of the ordinary. The most observable feature was the very great lack of birds, there being fewer than at any time Miss Wiley could remember. Attendance: 6. Leader: Farida A. Wiley.

**May 1. Serpentine Barrens, Chester Co., Pa.** The weather was showery in the A.M. Two of the largest and best known barrens in the country were visited. These outcrops of serpentine support a restricted but quite interesting flora. First stop was made at Unionville barrens located about eight miles southwest of West Chester. This barren is noted for its spectacular display of moss pink (*Phlox subulata*) and serpentine chickweed (*Cerastium arvense oblongifolium*). Despite the fact that the season was about two weeks ahead of normal, both the phlox and chickweed were in fine flower giving the area the appearance of being solidly covered with a pink and white carpet. Other plants observed in abundance here include *Senecio Smallii*, *Arenaria stricta* (both with abundant buds but not in flower), *Antennaria neodioica* (in flower) and *Saxifraga virginicensis* (in flower and fruit).

In the P. M. the group drove southward to the Nottingham barrens about five miles below Oxford, Pa., and near the Maryland border. This barren is quite different from the Unionville barrens in that it supports an arborescent growth, pitch pine (*Pinus rigida*), post oak (*Quercus stellata*), black-jack oak (*Q. marilandica*) all developing into fair sized trees. Also thickets of *Smilax rotundifolia* and various shrubs densely cover the area. Along the outer edge of the barrens were found the following: *Cerastium arvense oblongifolium* (in flower), *Arenaria stricta*, *Antennaria plantaginifolia* (in flower), *A. neglecta* (fruit fully mature), *Sisyrinchium mucronatum* (in flower), *Salix tristis* and *S. humilis* (both in fruit). Attendance: 7. Leader, Louis E. Hand.

**May 1. Van Cortlandt Park, N. Y.** Despite the threatening weather, the early time, and the several other Torrey Club trips scheduled for this date, the group set out for early flowering plants and migrating birds. Of the birds, 32 species were noted but apparently there had been no real migration during the night as very few warblers were seen. A great deal of the Van Cortlandt Park area is being dug up for roads and extension of the golf course, but the flowers were plentiful, as expected. A good stand of bluets (*Houstonia coerulea*) seem to be spreading in one section of the old nursery grounds which is interesting as this common plant is rare in Manhattan and Bronx. On a hill overlooking a public golf course, extensive stands of dutchman's breeches were noted. This hill holds most of the early flowering spring plants in rather large numbers: the common toothwort (*Dentaria laciniata*), early saxifrage (*Saxifraga virginicensis*). A few years ago the hill was covered with *Hepatica triloba* but this had disappeared, probably through picking. Nothing rare was seen and the trip ended as the rain began about twelve noon. Attendance: 4. Leader: William Rissanen.

**May 14-15. Camp Thendara on Lake Tiorati, Palisades Interstate Park, N. Y.** The New York Section of the Green Mountain Club was pleased to have a larger number of Torrey Botanical Club members than usual with them for their annual Bird Census at Camp Thendara on Lake Tiorati. The weather was perfect in every way, except for a short-lasting thunderstorm late Saturday afternoon. Neither species nor individual birds recorded came up to the number listed for last year. This seems to have been a condition reported from several other places as well. Vegetation was much farther advanced than has been usual for this census time. Hence, there was good botanizing for those who wished to study plants when no thrilling bird observation demanded attention. Beautiful vistas with lakes and mountains, both on the way to camp and from the spacious porch overlooking Tiorati, combined with abundant food served from the busy kitchen within the camp, made time pass all too quickly. This was pervaded by a friendly atmosphere of mutual interests and good fellowship and enhanced by the presence of our bird guide,

Mr. Howard H. Cleaves, noted lecturer and traveler, with his wealth of out-of-door experiences, which he generously shared with the group. This annual week-end outing of the Torrey Botanical Club and the New York Section of the Green Mountain Club is an event of long standing. May it continue to be an occasion looked forward to with pleasant anticipation in the years to come. Attendance: 15 Torrey members and guests. Leader: Laura Woodward Abbott.

**May 15. Terrace Pond, N. J.** The high point of the trip was a plentiful stand of a hepatic, *Riccardia multifida*, in fruit. At least it was *R. multifida* last fall. At this time of year it might be *R. palmata*! This was the first time any of us had seen the species in fruit and the leader was the only one present who had seen the species at all. We may describe it as fairly scarce hereabouts since all of us had been working on the hepatica for years. The leader was also able to show a lichen, *Arthonia gregaria*, in the only station known to him in northern New Jersey. Attendance: 4. Leader: G. G. Nearing.

**May 15. Shawangunk Mountain, N. Y.** Nature was very kind for this trip, in marked contrast to last year. Mr. Crabtree was under the weather, but his daughter pinched-hit for him. The *Rhodora* was in perfect form and several new stands were found. That and *Arenaria groenlandica* made the trip well worth while. There was an abundance of *Cypripedium acaule*. Leader: J. A. Crabtree.

**May 15. Forked River, N. J.** This was the seventh Torrey trip in the last decade to this splendid location and each visit has produced many new plants. Eighteen new species and one variety were observed on this trip. These additions along with four species and one variety reported by Hollis Koster, from collections made on former trips and just recently identified, make a grand total of 479 species. Localities visited on this trip were (1) thickets, open areas and meadows of State Game Farm and (2) Middle Branch bog and along railroad south of it. Among the new species seen on the trip was *Arisaema pusillum* (Peck) Nash. Some authorities make this small "Jack" a variety, form, or subspecies of *A. triphyllum*. It does however bloom several weeks later than the latter and grows in bogs. The colony of *Listera australis* discovered on the Club trip of June 21-22, 1947 has now increased to some two dozen or more thriving specimens, which were in full anthesis on this date. Also admired by the group were two plants of *Arethusa bulbosa* in full flower and of a strikingly deep pink hue. This is early for the fully developed specimens of this orchid. Attendance: 11. Leader: Louis E. Hand.

**May 29. Middletown, N. J.** We were too late for the bloom of *Pogonia verticillata* but saw many plants in fruit. The stand is healthy and appears to be spreading. The abundance of beech and the finding of several plants of *Orchis spectabilis* made this woodland seem more like north Jersey woods than like the coastal strip which extends southward. Attendance: 9. Guest leaders: Mrs. Martha Taylor and Mrs. Ruth Doremus.

**June 4. Morris Arboretum, Philadelphia, Pa.** A goodly crowd gathered at the Morris Arboretum where they were welcomed and botanically entertained by Dr. Schramm and Mr. Skinner. The herbarium was extremely interesting as were the trees of foreign origin—cedars, etc. Attendance: 25. Leaders: Dr. J. R. Schramm and Mr. Henry T. Skinner.

**June 5. Richmond, Staten Island, N. Y.** This date is a little early for the more interesting plants which can be seen in the sandy fields and salt marshes of this region. The dry conditions prevailing on the hillsides did not help matters any. In the marsh behind a church, a large stand of the false indigo, *Amorpha fruticosa*, was in full flower. There must be over fifty large shrubs of this plant growing well in a rather compact group. This stand is believed to have been planted by Mr. William T. Davis some years ago. Another plant which was noted growing abundantly in the same region and on the hillsides was alfalfa, *Medicago sativa*. It was conspicuous because of its unusual size, the majority of the plants being over or approaching a yard in height. A rare plant seen along the road was *Cerastium arvense* var. *oblongifolium*, growing in areas having serpentine rock such as this region has. Attendance: 9. Leader: William Rissanen.

**June 5. Oswego River, N. J.** The canoe trip was held as planned and thanks to everybody concerned, Miss Williams, Hack's Canoe Retreat, and the perfect weather, it was

even better than the previous one. We stayed our departure for some time waiting for a car which got lost. The length of the trip and the short time prevented the botanizing we would like to have done. Though who could have missed the continuous stand of southern white cedar on either bank of the stream or the broad expanse of Martha bog and the higher and dry pine forest in the background? Only two canoes were upset and that caused nothing but a slight wetting. It was arranged to have cars at each end of the trip so there was no paddling up stream. Attendance: about 20: Leader: Marion Williams.

**June 12. Elysian Lodge to Sunfish Pond, Warren Co., N. J.** This was the second Club trip over this route; the initial trip being August 10, 1941. The weather was clear and very hot. From the Elysian Club, group followed abandoned Kaiser Road to the ridge crest and thence southward, along the Appalachian Trail, to Sunfish Pond. Return by same route; round trip distance, six and one half miles. A brook parallels Kaiser Road for a short distance at the start and some northern plants were seen there, including *Acer pennsylvanicum*, *Betula lutea*, *Rhododendron mazimum*, *Viola rotundifolia*, etc. Farther along Kaiser Road but below the ridge crest *Arabis canadensis*, *Scrophularia leporella*, *Galium lanceolatum*, *Panicum Boscii*, *Castilleja coccinea*, and other plants were found in flower. In addition to plants, the advance members of the party surprised a red fox, which quickly took to the underbrush. On the A. T. proper, nine new species were added to the trail list for this section. Best find was a colony of paper birch (*Betula alba papyrifera*) at Tock Swamp. On the previous trip this was passed by for *B. populifolia* on account of the dark "stained" bark which gave it an unnatural appearance. The characteristic ovate leaves however quickly revealed its identity this time. Two plants of *Rhodora* (past flowering) were found and a number of plants of *Cornus canadensis* were still in flower. A short distance along the trail a small red spruce was seen with more and larger specimens back in the swamp. Also off the Trail, a small colony of *Coptis trifolia* was seen in fruit. Due to heat haze, the usual spectacular distant views from the various exposed sections of ridge were not obtained. Attendance: 17. Leader: Louis E. Hand.

**June 19. Watchung Reservation, N. J.** This trip was for the purpose of determining the hepatic flora in the Watchung Reservation in Union County, N. J., as the Union County Park Commission is preparing a list of all plants and animals found within the Reservation. Dr. H. N. Moldenke of the New York Botanical Garden is in charge of the botanical survey and specimens collected on this trip will be sent to him. In a visit to this region last summer the leader had found a large stand of *Metzgeria conjugata* in a cool ravine, and we found it still plentiful on the sides of the moist cliffs on this trip. A better find was *Lejeunea cavifolia*, a not too common plant. This specimen does not answer to the type as described in Frye & Clark's *HEPATICAE OF NORTH AMERICA*, but seems to be intermediate between the type and its variety *planuscula*, lacking the numerous oil cells required in the type but having larger underleaves than elsewhere in the park. The other liverworts collected or seen were: *Lophocolea heterophylla*, *Anthoceros laevis*, *Pellia epiphylla*, *Calypogeia trichomanis*, *Cephaloxia bicuspidata*, *Plectocolea hyalina*, *Odontoschisma denuatum*. In the afternoon the members came to the Museum in the Park and discovered that Mrs. Gladys P. Anderson, a member of the Torrey Club, was to give a talk on the flower families. So we joined their meeting. Attendance: 9. Leader: William Rissanen.

**June 26. Allaire, N. J.** Due to the heat and distance only six reported for the trip and very little was done in the way of botanizing. As yet the State has done nothing to develop the park though they do have a caretaker. The list of plants is growing slowly. Attendance: 6. Leader: V. L. Frazee.

# INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

## TAXONOMY, PHYLOGENY AND FLORISTICS

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